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REVIEW OF SOUTH AMERICAN CHARACID FISHES OF SUBTRIBE NANNOSTOMINA [1]

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Introduction

Fishes of the subtribe Nannostomina, family Characidae, form a clearly definable group of about nine small South American freshwater fishes. No member is known over 44.5 mm. in standard length. They appear restricted in habitat to shaded forest brooks, seepages, and ponds, and are apparently confined to the Guianas, Río Orinoco in Venezuela, and the Amazon Basin of Brazil, Peru, Colombia, and Bolivia. All of the known species have been imported into Europe or North America as aquarium fishes. In the aquarium trade they are known as pencil fishes.

The osteology and relationships of these fishes have been treated elsewhere (Weitzman 1964), and their intercharacid relationships will be but briefly mentioned here. They are members of the characid subfamily Lebiasininae, which consists of two tribes, the Lebiasinini and the Pyrrhulinini. The Pyrrhulinini comprises two subtribes, the Pyrrhulinina and the Nannostomina. The Nannostomina appears to be the most specialized group within the Lebiasininae.

[1] This paper is the third and final of three parts based on a Ph. D. dissertation submitted at Stanford University, Calif. See Weitzman (1962, 1964) for the two preceding parts.

The Lebiasinini and Pyrrhulinina are small to moderate-sized, predaceous characids with moderate-sized mouths. The tiny mouths of members of the Nannostomina, however, are adapted for feeding on very small organisms. They apparently feed primarily on animals that occur on plants, rocks, and other objects and also to some extent on slowly moving, free-swimming organisms.

Wickler (1957) has described the breeding behavior of certain of these fishes in a preliminary fashion, and there is a very large amount of literature on this subject published by aquarists. However, even though they are excellent aquarium subjects, no detailed behavioral study has been published about them. A breeding pair enters a group of fine-leaved plants or a clump of roots, the male presses its body against that of the female, curves its anal fin around the female's vent, and the female sheds one to a very few eggs. The structure of the male's anal fin in several species is modified for aiding fertilization by guiding sperm over the female's vent. At this time the male sheds an undetermined number of sperm and fertilizes the eggs. The eggs are very slightly adhesive and may become attached to plants or fall to the bottom. All the species that I have seen alive (all but *Nannostomus digrammus* and *Nannostomus bifasciatus*) lay eggs of about 0.6 to 0.7 mm. The young mature in 8 to 10 weeks and specimens may live for as long as 4 years. Their lifespan in aquaria is usually 2 or 3 years.

Since most of Nannostomina can be bred with relative ease, they would make fine subjects for comparative ethological studies. It would be interesting to compare the taxonomic implications of such studies with those derived from the morphological investigation presented here.

The spotty locality records of the Nannostomina, the frequent damaged condition of the specimens, and the paucity of specimens from many localities have precluded satisfactory use of statistical procedures in analyzing geographical population differences or in recording changes in body proportions correlated with growth. Collectors frequently have packed these small, delicate fishes with specimens of other, larger species with the result that the nannostominans have been squashed out of shape, making valid measurements impossible. Only specimens in reasonably good condition were measured. For this reason, counts should be considered more reliable than measurements in the data presented below. The data available indicate in several instances that many geographically distinct populations of these fishes probably exist. Some of these differences are pointed out in the discussion under each species. It would be foolish to designate these different population samples as subspecies in view of the inadequate number of specimens and data

at hand. The primary function served by this paper is to point out our present state of knowledge concerning these fishes and to indicate problems for future study.

Counts and measurements were taken from the left side of each specimen. In the descriptions the initial values are the arithmetical means, and the values included in parentheses are the extremes of all specimens cited in the material examined. Measurements were taken from adult specimens only.

The following straight-line measurements were made from the anteriormost part of the fleshy tip of the upper jaw to some point posterior on the body surface. Standard length (SL) was measured to the posterior end of the hypural fan. Predorsal length was measured to the anterior base of the first dorsal fin ray. Preanal length was taken to the anterior base of the most anterior, visible anal fin ray. Head length was measured to the most posterior border of the opercular bone, not the fleshy flap which was often damaged.

Eye length is the greatest distance between the posterior border of the first infraorbital and the anterior border of the fifth infraorbital bone. Depth was measured from the anterior dorsal fin base vertically to the median profile of the belly. Least depth of caudal peduncle was measured vertically. Length of caudal peduncle was measured from the posterior base of the last anal fin ray to the posterior end of the hypural fan. Interorbital width is the least width between the lateral supraorbital borders of the frontal bones.

Vertebral counts were taken from radiographs and include the vertebrae forming the pars sustentaculum of the Weberian apparatus and the ultimate vertebra with its urostyle.

Fin counts: The ultimate (posterior) ray of the dorsal and anal fins was counted as one when one ray was associated with the last pterygiophore and as two when there were two entirely separate rays associated with the last pterygiophore. Counts were least variable when this method was employed. All anterior rudiments of fin rays were counted. Unbranched rays (except the most posterior ray of the dorsal, anal, pectoral, or pelvic fins) are designated by lowercase roman and branched rays by Arabic numerals. The principal caudal fin ray count includes all rays associated with the hypural elements and may be taken without recourse to examining the hypural fan by counting all branched rays and adding two. The count of the upper lobe is given first, followed by a bar (/) and then the count of the rays of the lower caudal lobe.

Gill-raker counts in these small fishes can be made most accurately on alizarin-stained specimens and all such counts were confined to such specimens. The counts are of the bony supports of gill rakers. Scale counts in a lateral series refer to all scales in a median lateral

series extending to the posterior midbase of the hypural fan. Vertical scale rows are counted between the anterior parts of the dorsal and anal fin bases.

Although the Nannostomina as a whole are easily definable and the species readily separable, their segregation into generic groups having a clear phylogenetic basis has not proven easy. However, some indication of their possible phylogenetic history is provided by their morphology, and morphological definitions of two generic groups is possible. Of the characters that seem to have generic and specific significance, the following appear to be most important.

Anal fin: The anal fin of males of this subtribe is used as an accessory sexual organ to guide the sperm toward the female's vent. During the spawning act, the anterior, posterior, and distal parts of the fin are cupped to form a bowl that partially covers the female's vent, apparently directing the sperm toward the eggs as they are laid. Correlated with this function is a previously overlooked morphological fact. The individual anal fin rays of the males of several species are widened in the sagittal plane (figs. 4 and 6). This modification is also found to a certain extent in some members of the subtribe Pyrrhulinina, the closest living relatives of the Nannostomina. This feature seems to have more significance at the specific than at the generic level.

Infraorbital bones: The usefulness of these structures also has been overlooked by previous authors. There are two types of infraorbital bone arrangement in the subtribe. In one they are more elongate, and both the first and second elements have a bony infraorbital canal. In the other type, the first two infraorbitals are short and the second is without a bony canal. The closest relatives of the Nannostomina, the Pyrrhulinina, have a canal in both the first and second infraorbital bones; its absence in the second infraorbital of some Nannostomina is possibly a neotenic specialization. This character is considered here to have generic significance because it is consistent and correlated with a definite difference in snout and head shape.

Color: The melanophore patterns occurring in this subtribe can be separated conveniently into three categories.

The first of these consists of long, dark, horizontal stripes present in almost all species. The term stripe is restricted in this account to the elongate pigmented areas that extend in a horizontal direction on the sides of these fishes. There are several of these stripes as follows: Primary stripe, the main midside stripe usually extending from the snout to the eye, across the operculum to the lower part of the caudal peduncle and onto the caudal fin. Secondary stripe, the dark stripe above the primary stripe. It usually extends from the nape or the top of the head to the upper portion of the caudal peduncle.

It often blends with the darkly pigmented back. Tertiary stripe, the lowermost stripe often extending from the lower jaw, across the lower part of the operculum, below the base of the pectoral fin to the origin of the anal fin. Additional stripes occur on some species, such as *Poecilobrycon eques*. Live specimens suddenly illuminated at night may show the stripes only faintly or almost not at all. During the day these same stripes are darkly pigmented.

The second category consists of oblique bands. The anterior of these lies along the sides a short distance anterior to the dorsal fin, while the posterior lies along the midside a short distance posterior to the dorsal fin. These oblique bands are usually absent or extremely pale in living specimens during the daylight hours; however, in the absence of light the oblique bands become very dark. Females of *Nannostomus beckfordi* while spawning often will show faintly the oblique bands. The oblique bands appear in some species, such as *N. beckfordi*, to be mostly areas of the primary horizontal stripe which fail to become pale under the influence of darkness. However, even in this species these bands are a little more than this because some of the area of the oblique band occurs above the primary horizontal stripe. In such species as *Poecilobrycon eques*, much of the area of the oblique bands is above the primary horizontal stripe.

The oblique bands have been called "night paint" by Hoedeman (1950) because they are usually present only at night. Specimens of *N. beckfordi* preserved at night in ten percent formalin retain their "night pigment" pattern. In these specimens the oblique bands are quite dark and their horizontal stripes are faded and sometimes indistinct.

In specimens preserved in daylight, oblique bands are present often but are usually very pale. Horizontal stripes are almost always present and distinct except on faded specimens or specimens preserved at night. Care should be used in determining the presence or absence of oblique bands from preserved specimens because if, as is usually the case, the specimens were preserved during daylight hours, the pigment of the melanophores of the oblique bands may be so contracted that the bands do not show.

Permanent blotches constitute the third category. These are present in only one species, *Nannostomus espei*, and differ in position and quality from all other dark markings seen in the other species. They are permanent, not disappearing in daylight or darkness, although as with other pigment, they may fade slightly at night. The borders of the blotches are darker than the rest of the blotch. This is not true of the oblique bands. There are five such permanent blotches along the midsides on *N. espei*, the first above the pectoral fin, the second below the origin of the dorsal fin, the third midway between

the origin of the pelvic fin and the anal fin, the fourth above the anal fin origin, and the fifth in the lower half of the caudal fin root.

Caudal fin rays and body swimming position: The normal principal caudal ray count is 10/9 in characids, and this is true of all Nannostomina examined by me. However, in two species, two of the rays normally in the upper lobe of the caudal fin have their distal ends in the lower lobe. The proximal ends of these two rays retain the normal position on the hypural fan and thus originate in the upper lobe. The two species having this arrangement swim at an inclined angle, head up. Steindachner (1876) first noticed that the lower caudal fin lobe is larger in some Nannostomina, and Hoedeman (1950) noted that these unequal lobes are correlated with the swimming position. Hoedeman did not describe accurately the morphological arrangement of the caudal fin rays. He stated that there is a difference in the shape of the swim bladder correlated with the swimming position. This is possibly true, but investigation of this feature has been postponed pending a histological examination of the swim bladder and its musculature. A comparative histological examination of the semicircular canals and associated structures probably would show also interesting morphological differences associated with the oblique swimming position. Braemer and Braemer (1958) have begun to investigate some of the morphological differences in the arrangement of statoliths in characids, including that in *Poecilobrycon eques*, one of the oblique swimmers.

Other characters have been reported to have generic significance in Nannostomina. For example, Eigenmann (1909) based *Poecilobrycon* mainly on the presence of an adipose fin in the type species, *P. harrisoni*. However, additional specimens have shown that members of this species may or may not have an adipose fin, and the character is of no generic significance in this group. Steindachner (1876) noted that the adipose fin is variably present in *Poecilobrycon eques*. Hoedeman (1950) attempted to use the shape of the teeth as a generic character, but their shape often varies from individual to individual as well as among different geographical populations of the same species.

The characters most useful in separating species are color pattern, scale counts, gill-raker counts, numbers of vertebrae and teeth, and body proportions. Preliminary observations of living specimens in aquaria indicate that behavior also may be of considerable aid in understanding specific and generic relationships.

The synonymy used here is selected, and no attempt has been made to include all references to these fishes that have appeared in the

very extensive aquarium literature. Many references to the aquarium literature concerning these fishes can be obtained from Hoedeman (1950).

The following abbreviations are used:

AM	Zoological Museum, Amsterdam
ANSP	Academy of Natural Sciences, Philadelphia
CAS	California Academy of Sciences
CAS (IUM)	Specimens formerly at the Indiana University Museum and now at the California Academy of Sciences but still bearing Indiana University Museum numbers
CNHM	Chicago Natural History Museum
MCZ	Museum of Comparative Zoology, Harvard
USNM	United States National Museum

For loan of specimens I am indebted to Dr. George S. Myers of Stanford University, W. I. Follett of the California Academy of Sciences, Loren P. Woods of the Chicago Natural History Museum, Dr. Giles Mead of the Museum of Comparative Zoology, Harvard University and Dr. James Böhlke of the Academy of Natural Sciences of Philadelphia. I am indebted greatly to Dr. George S. Myers for numerous discussions and for critically reading the original manuscript. In addition the following people have read the manuscript at various stages, all offering useful advice and aid: Drs. Paul Erlich, Myra Keen and Warren Freihofer of Stanford University, Mrs. Lillian Dempster of the California Academy of Sciences, and Drs. Robert H. Gibbs, Jr., and Victor G. Springer of the U.S. National Museum.

I am indebted also to Gen. Thomas D. White for forwarding living specimens of *Nannostomus marginatus* from eastern Colombia so that I could record their life colors. All drawings are by the author with the exception of figure 6, the anal fin of a male *Nannostomus digrammus* prepared by Dr. Margaret Bradbury.

The work was begun and largely completed at the Department of Biological Sciences, Stanford University. Additional work was done at the Department of Anatomy, Stanford University, and the U.S. National Museum, Smithsonian Institution.

Note on figures: Figures 1, 2, 4, 5, 7, 8, 9, 11, and 12 show male specimens with the antorbital and first three orbital bones and the third set (counting from the anterior end of the jaw base) of upper (premaxillary) and lower (maxillary) teeth. The enlarged scale (or scales) is from the third longitudinal scale row of the left side, just below the dorsal fin except where noted in the text. These parts are all drawn from alizarin specimens.

Key to Genera and Species of Subtribe Nannostomina

1. Second infraorbital bone without bony canal passing in its substance. Genus **Nannostomus.** 2

   Second infraorbital bone with well-developed bony infraorbital canal passing in its substance . . . . . Genus **Poecilobrycon.** 7

2. Very indistinct primary horizontal stripe present. Secondary or tertiary horizontal stripes absent. Five dark permanent blotches along sides (in life these blotches not fading during exposure of fish to daylight). **Nannostomus espei** (p. 9)

   Primary horizontal stripe present, very well developed. Some species with secondary and tertiary horizontal stripes present. One or two pale oblique bands on sides (in life these bands ordinarily present only when fish kept in dark). Permanent blotches absent 3

3. Primary horizontal stripe present, secondary stripe present or absent, tertiary horizontal stripe absent. Teeth in single row on premaxillary, 5 to d (usually 6). Anal fin rays of males slightly to greatly modified, flattene6 in sagittal plane. 4

   Primary, secondary, and tertiary horizontal stripes well developed. Teeth in one row on premaxillary, 7 to 8 (usually 8). Anal fin rays of males completely unmodified in appearance 6

4. Perforated scales in lateral line 2 to 4. Adipose fin absent. Anal fin rays iii,9. Anal fin rays of males relatively little modified, not greatly flattened and expanded in sagittal plane 5

   No perforated lateral line scales. Adipose fin present. Anal fin rays iii,8. Anal fin rays of males greatly modified, flattened, and expanded in sagittal plane . . . . . **Nannostomus digrammus** (p. 22)

5. Secondary horizontal stripe absent. Gill rakers 9 to 10+17 to 18. **Nannostomus bifasciatus** (p. 19)

   Secondary horizontal stripe present. Gill rakers 8+14. **Nannostomus beckfordi** (p. 12)

6. Scales 26 to 27 in lateral series. Total vertebrae (including those of Weberian apparatus) 35 to 36. Adipose fin present, either well developed or rudimentary. About 11 teeth in second tooth row of dentary. Snout in eye 1.0. Least depth of caudal peduncle in standard length 10.0 to 10.4. **Nannostomus trifasciatus** (p. 29)

   Scales 21 to 23 in lateral series. Total vertebrae 31 to 33. Adipose fin absent. Teeth in the second row of dentary 6 to 7. Snout in eye 1.3 to 1.4. Least depth of caudal peduncle in standard length 7.8 to 8.5. **Nannostomus marginatus** (p. 32)

7. Principal caudal fin rays 10/9, their distribution in lower and upper caudal lobes normal, 10 ending in upper lobe, 9 ending in lower lobe. Total vertebrae 38 to 39. Length of caudal peduncle in standard length 5.3 to 6.1 . . . (Subgenus *Poecilobrycon*). **Poecilobrycon harrisoni** (p. 38)

   Principal caudal fin rays 10/9, but 8 rays end in upper lobe and 11 in lower lobe of caudal fin. Total vertebrae 33 to 34. Length of caudal peduncle in standard length 6.0 to 7.5 . . . . . (Subgenus *Nannobrycon*). 8

8. Scales 28 to 30 in lateral series. Perforated scales in lateral line 2 to 5. Adipose fin present. Gill rakers 9+14. Inner tooth row of dentary absent; teeth in outer dentary tooth row 6 to 7. **Poecilobrycon unifasciatus** (p. 42)

Scales 24 to 25 in lateral series. No perforated lateral line scales. Adipose fin present or absent. Gill rakers 16+24. Teeth in inner dentary row 12; teeth in outer dentary row 9 . . . . . **Poecilobrycon eques** (p. 47)

Genus *Nannostomus* Günther

Nannostomus Günther, 1872, p. 146 (type species: *Nannostomus beckfordi* Günther, 1872, by monotypy).

Diagnosis.—Among the Lebiasininae the following character appears unique for this genus: Second infraorbital bone without bony canal for infraorbital branch of laterosensory canal; in addition, snout short, 1.0 to 1.4 in eye diameter. Correlated with the short snout, *Nannostomus* has a shorter, broader ethmoid and vomer, a shorter antorbital and infraorbital, and a shorter mesopterygoid and nasal bone than *Poecilobrycon*. An adipose fin may be either present or absent. Either the primary or tertiary, or both primary and tertiary horizontal stripes may be present or absent. The anal fin rays of the males may be greatly modified or scarcely modified as an accessory organ. The body is short to fairly elongate, the depth being 3.5 to 5.0 in the standard length.

The name *Nannostomus* is derived from the Greek *νανοσ*, meaning little or dwarf, and *στομα*, meaning mouth.

Nannostomus espei (Meinken)

Figure 1

Poecilobrycon espei Meinken, 1956, p. 31 (original description; no type locality; types in collection of Meinken and at Stanford University, lectotype SU 51593).

Nannostomus espei—Böhlke, 1956, p. 2 (description; unnamed creek emptying into the Paruma River, a tributary of the Kamarang River, which empties into the Mazaruni River, British Guiana).—Sterba and Tucker, 1962, p. 213 (description and aquarium notes).

Diagnosis.—Secondary and tertiary horizontal stripes absent; primary horizontal stripe poorly developed; permanent blotches on sides of living specimens (blotches do not disappear during daytime); scales (fig. 1) very much in outline like scales of members of subtribe Pyrrhulinina (see description on page 12). *Nannostomus espei* differs from all members of subtribe Nannostomina except *Nannostomus marginatus* by having fewer than 23 scales in lateral series.

Description.—Body elongate, sides flattened, and body compressed posteriorly. Greatest depth between posterior tip of appressed pectorals and anterior part of base of dorsal fin. Standard length of largest specimen examined, 28.1 mm. Greatest body depth 4.3 in all specimens; least depth of caudal peduncle 9.6 (9.4 to 10.0); length of caudal peduncle of both sexes 6.4 (6.1 to 7.0); snout tip to origin of dorsal 1.9 (1.9 to 2.0); snout tip to origin of anal 1.3 in all specimens.

Head elongate, snout obtuse in vertical and horizontal profiles. Top of head very slightly convex between eyes. Head 3.6 (3.5 to 3.7); eye in head 3.0 (2.9 to 3.0); snout in eye about 1.0 in all specimens examined; least width of bony interorbital in greatest eye diameter 1.0 or very slightly less in all specimens examined.

Premaxillary with 7 teeth. Each tooth except posterior 1 or 2 with 5 cusps. Posterior 2 teeth usually quadricuspid. Sometimes most anteromedial premaxillary tooth with only 4 cusps. Usually with largest cusp just medial to farthest posterolateral cusp. Maxillary with single, uni- to quadricuspid tooth. Teeth in anterior row of each dentary 7 to 8. Anterior 5 or 6 teeth hexacuspid, third from anteromedial cusp largest. Posteriormost dentary tooth usually tricuspid. Second dentary tooth row with 8 to 11 unicuspid teeth. Gill rakers 10+17 on each first gill arch in one alizarin preparation, SU 50252.

Dorsal fin rays ii,8; anal iii,9; pectoral i,10; pelvics ii,7, in all specimens examined. Adipose fin present, well developed in all specimens. Caudal fin with principal rays 10/9; distal tips of all ray elements of first (upper) 10 principal rays within upper caudal lobe; remaining 9 principal rays end in lower lobe.

Male's anal fin modified (fig. 1); rays somewhat expanded and more similar to highly modified anal rays of *Nannostomus digrammus* than any other species of Nannostomina.

Radial grooves of scales in third horizontal scale series below dorsal fin shown in figure 1. Posterior field of each scale with 2 to 3 radial grooves; dorsal and ventral fields each with 1 radial groove; anterior field with 2 to 4 radial grooves. Dorsal and ventral anterior corners of scales in this species more acute than in any other species of Nannostomina. Acute corners very similar to those found in subtribe Pyrrhulinina. Scales in lateral series 22 in all specimens examined. Perforated lateral-line scales on each side 1 or 2. Scales in median predorsal series 10 in all specimens examined. Total number of vertebrae 33 (18 precaudals and 15 caudals) in all specimens.

Color in alcohol.—Preserved specimens (SU 50214) have the following color: Top of head light to dark brown. Primary horizontal stripe from tip of snout across maxillary and first obrital bones onto anterior part of iris of eye; then from posterior part of iris to edge of opercular bone. Posterior to eye, primary horizontal stripe somewhat diffuse and hard to distinguish. Primary horizontal stripe behind operculum represented as very diffuse, slightly darkened area extending posteriorly to caudal peduncle, through third and fourth longitudinal scale rows. (In live specimens kept in an aquarium with dark brown peatmoss bottom and subdued light, horizontal stripe became much darker but remained diffuse.) Large permanent blotches

5 on sides with slightly irregular margins as shown in figure 1. Borders of blotches (very different from oblique bands described in other species) slightly darker than their centers. Very pale stripe above blotches and above very light and diffuse primary horizontal stripe. Dorsum brown above pale stripe. Network of dark lines that follow scale edges superimposed on entire body pigment pattern. Belly white, all fins hyaline.

Color in life.—Life colors of an aquarium specimen as follows: Five large permanent blotches dark brown to almost black. Body color very light brown with slight greenish cast. This ground color darker on back. Abdominal region silvery. Light green, somewhat iridescent stripe extending along sides just above dorsal borders of permanent blotches. This stripe reflecting pale gold. Fins translucent except for few dark spots on anal fin.

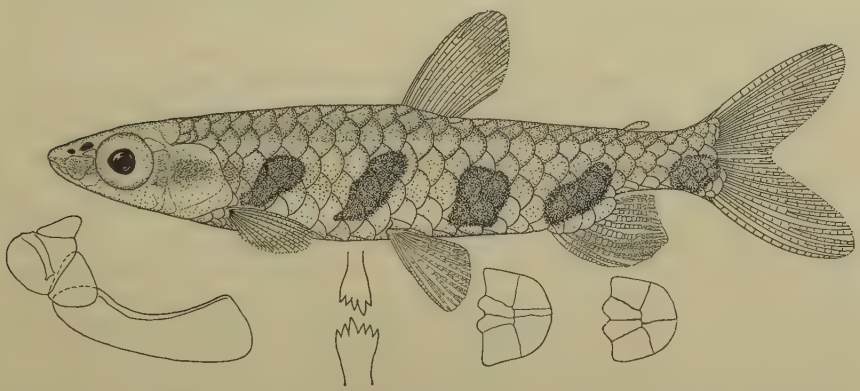

Figure 1.—*Nannostomus espei*, male, SL 27.6 mm., SU 50214 (see text for discussion of scales).

Remarks.—The original description of this species was inadequate, and no types were designated. Also because the type locality was unknown, none was cited. Böhlke (1956) has located and published data on the collecting site of the original aquarium importation of this species, but did not designate a restricted locality—this is done here. The "restricted locality" is that given by Böhlke (1956, p 1). This locality, along the Paruma River, is apparently in the vicinity of lat. 5°50′ to 55′ N., long. 61°05′ to 10′ W. At my request, Herr Meinken has sent to me three of the specimens used in his original description. One of these (SU 51593), an adult female 26.5 in SL, is here designated as the lectotype. The two other specimens, paralectotypes, one an adult female 28.5 mm. and one subadult female 21.0 mm. in SL, now bear the number SU 51592.

The color pattern of *Nannostomus espei* greatly resembles that of *Pyrrhulina vittata* Regan and *Pyrrhulina spilota* Weitzman. Many of the scales of *Nannostomus espei* are more like those in the genera *Pyrrhulina, Copeina,* and *Copella* than those of other species of *Nannostomus* or *Poecilobrycon.* In figure 1, the scale to the left is from the third longitudinal scale row, just below the dorsal fin. It is typically pyrrhulininan in outline. That to the right is from the second longitudinal row near the adipose fin and is typically nannostominan in outline. The phylogenetic significance of these facts is not understood, especially since this species has the typical osteology of *Nannostomus.* It seems possible that this species has retained a few primitive features that were present in its presumably somewhat more *Pyrrhulina*-like ancestors. This species also has a body form which suggests that of the subtribe Pyrrhulinina more than the body form of any other species of *Nannostomus* or *Poecilobrycon.* The body form of *Nannostomus* and *Poecilobrycon* is usually more or less smoothly fusiform, whereas that of *Pyrrhulina* is not, the profile showing a slight notch behind the dorsal fin and the belly being slightly flat. *Nannostomus espei* has the dorsal notch of *Pyrrhulina.* This body shape in *espei* is subtle and considerable experience with live and preserved specimens was necessary before it was detected.

Specimens examined.—Five (one alizarin preparation), ANSP 73873, SL 21.5–28.1 mm., British Guiana, an unnamed creek, tributary to the Paruma River, a tributary of the Mazaruni River via the Kamarang River, Pakaraima Mountain region of western British Guiana, lat. 5°50′–55′ N., long. 61°05′–10′ W., 1955, Louis Chung.—One alizarin preparation, SU 50252, SL 25.0 mm., aquarium specimens, locality unknown but probably British Guiana.—Seven, SU 50214, SL 25.5–27.0 mm., aquarium specimens, locality unknown but probably British Guiana.—One, SU 51593 (lectotype) and two, SU 51592, paralectotypes, for locality see discussion on page 11.

Nannostomus beckfordi Günther

Figures 2, 3, 4

Nannostomus beckfordi Günther, 1872, p. 146 (original description; type locality: Goedverwating, a plantation on the coast of Demerara, British Guiana; holotype in British Museum [Natural History]).—Eigenmann and Eigenmann, 1891, p. 49 (listed).—Eigenmann, 1912, p. 281 (copied description).—Hoedeman, 1950, p. 16 (description; no specimens listed).—Boeseman, 1954, p. 18 (Surinam).

Nannostomus anomalus Steindachner, 1876, p. 129 (original description; type locality: mouth of Rio Negro, Brazil; types in Vienna Museum).—Eigenmann and Eigenmann, 1891, p. 49 (listed).—Eigenmann, 1910, p. 427 (listed).—Meinken, 1931, p. 554 (description from life; figure).—Innes, 1935 and later editions, p. 153 (description from life; photograph).—Puyo, 1949, p. 117 (description; Cayenne Island, French Guiana).—Boeseman, 1952, p. 184 (Surinam); 1953, p. 16 (Surinam).—Axelrod and Schultz, 1955, p. 239 (description and aquarium notes).

Nannostomus minimus Eigenmann, 1909, p. 42 (original description; type locality: Erukin, British Guiana; holotype in Chicago Natural History Museum); 1910, p. 427 (listed); 1912, p. 282, pl. 36, fig. 5 (description).

Nannostomus simplex Eigenmann, 1909, p. 42 (original description; type locality: Lama Stop-Off, British Guiana; holotype in Chicago Natural History Museum); 1910, p. 427 (listed); 1912, p. 283, pl. 36, fig. 6 (description).

Nannostomus beckfordii.—Eigenmann, 1910, p. 427 (listed, name emended).

Nannostomus beckfordi surinami Hoedeman, 1954a, p. 84 (original description; type locality: Berg en Dal at Surinam River, Surinam; holotype in Zoological Museum of Amsterdam).

Nannostomus aripirangensis Meinken, 1931, p. 553 (original description; figure; type locality: Brazil, State of Pará, Aripiranga Island NE. of Belém do Pará; types destroyed during World War II, Meinken in litt.).—Axelrod and Schultz, 1955, p. 240 (copied description and aquarium notes).—Sterba and Tucker, 1962, p. 210 (description and aquarium notes).

Nannostomus beckfordi aripirangensis.—Hoedeman, 1950, p. 18 (copied description); 1954a, p. 84 (listed).

Nannostomus beckfordi anomalus.—Sterba and Tucker, 1962, p. 210 (description and aquarium notes).

DIAGNOSIS.—This species possesses few characters not found in at least some of the other members of the genus *Nannostomus* and is therefore difficult to diagnose by any single characteristic. Perhaps the best single diagnostic character complex is the pattern of horizontal stripes.

Secondary and tertiary horizontal stripes absent; well-developed primary horizontal stripe present; few (2–6) perforated lateral line scales present; 9 to 10+17 to 18 gill rakers; iii,9 anal fin rays; and 23 to 26 scales in a lateral series.

DESCRIPTION.—Body slender, cylindrical except in region of moderately compressed caudal peduncle. Greatest body depth slightly anterior to dorsal fin origin. Standard length of largest specimen 29.6 mm. Greatest body depth 4.3 [3.5 in egg-filled females] to 5.0 [in apparently starving specimens]; least depth of caudal peduncle 9.9 (8.8–10.8); length of caudal peduncle of population sample from Obidos (CM 19648) 5.2 (4.9–5.6), of population from Uruará Brook (SU 50257) 6.0 (5.5–6.3); length of caudal peduncle of all specimens measured 5.8 [a rather meaningless figure since the measurements are biased toward a large number of specimens from Uruará Brook, SU 50257] (4.9–6.3); snout tip to origin of dorsal fin 1.85 (1.62–1.99); snout tip to origin of anal fin 1.30 (1.24–1.35).

Head conic; snout blunt, obtuse in vertical and horizontal profile. Head 3.8 (3.5–4.0); eye in head 2.8 (2.5–3.2); snout in eye 1.24 (1.05–1.39); least width of bony interorbit in greatest eye diameter 1.1 (1.04–1.19).

Premaxillary with 6 teeth; anterior teeth quinquecuspid, lateral teeth quinque- to septemcuspid. [There is some geographical variation in the prominence of the individual cusps; for example specimens

from Baduel, French Guiana, SU 50259, and specimens from Uruará Brook, SU 50257, have all the cusps of the premaxillary teeth about equal (fig. 2). Specimens from Obidos have the second cusp from posterolateral side much enlarged, quite similar to the upper left tooth shown in the figure of *Poecilobrycon eques* (fig. 12)]. Maxillary with single uni- to octocuspid compressed tooth, cusps subequal. Dentary with 5 to 6 teeth (almost always 6 in all population samples examined). Teeth in anterior dentary tooth row quinque- to sexcuspid (usually sexcuspid). Specimens from Uruará Brook with subequal cusps; however, specimens from Obidos with centralmost cusp enlarged in anterior 4 to 5 teeth of dentary. Teeth 2 to 6 in inner tooth row of dentary (seen in alizarin preparations only). Gill rakers 9 to 10+17 to 18 (seen in alizarin specimens only).

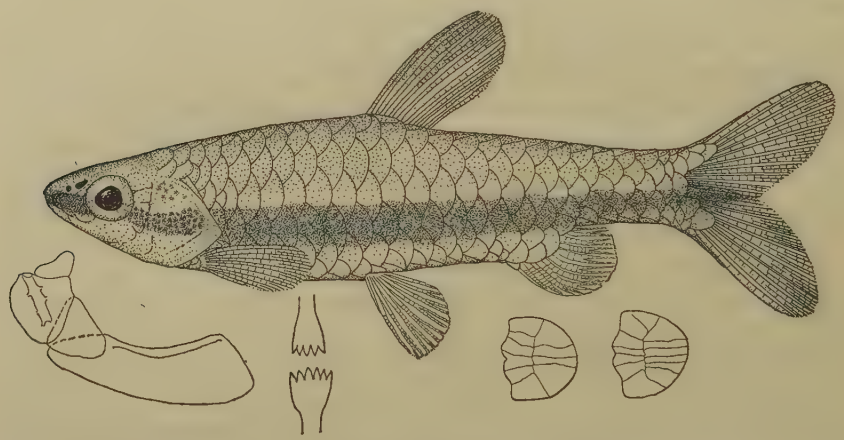

FIGURE 2.—*Nannostomus beckfordi*, male, SL 30.0 mm., SU 50261 (both scales are from third longitudinal row, below dorsal fin).

Dorsal fin ii,8; anal fin iii,9; pectoral i,10 to i,12; pelvic fin ii,7. Adipose fin absent in all specimens examined. Principal caudal fin rays 10/9; distal tips of all elements of first 10 rays contained in upper caudal lobe, distal tips of remaining 9 principal rays in lower lobe. Male with anal fin (figs. 2 and 4) somewhat modified in same manner as extremely modified anal fin of *N. digrammus*. Anal fin of female (fig. 3) unmodified. [Observation of living male *beckfordi* shows that while courting and spawning, the male often cups the fin into a spoon-shaped bowl and that, while spawning, the male places his fin partially over the female's vent.]

For radial grooves of scales in median scale row below dorsal fin, see figure 2. Posterior field with 2 to 6 radial grooves; dorsal and ventral fields with 1 or 2 radial grooves; and anterior field with 3 to

7 radial grooves. Scales in lateral series 24 (23–26); perforated lateral line scales 2 to 6 (usually 4 in population from Uruará Brook). Specimens often damaged so heavily that scales impossible to count accurately. In all instances, intact specimens from other localities with only 4 to 6 perforated scales. Scales in median series anterior to dorsal fin 10–11. Specimens from Uruará Brook with following total vertebral counts: 6 specimens with 34; 19 with 35 vertebrae. Specimens from Obidos: 3 specimens with 33, 31 specimens with 34 vertebrae, 8 specimens with 35 and 2 specimens with 36 vertebrae. Most specimens from other localities with 35 vertebrae. Usually 18 to 20 precaudal vertebrae and 15 to 16 caudal vertebrae, always in combination to produce total of 33 to 36 vertebrae. Counts of vertebrae undoubtedly will prove useful in distinguishing and determining subspecies.

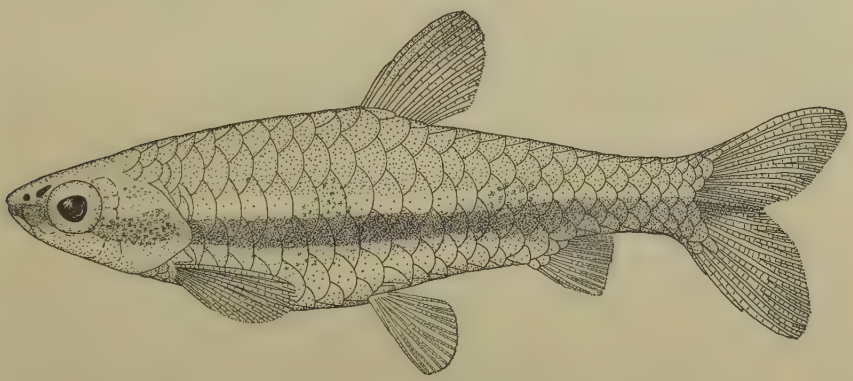

FIGURE 3.—*Nannostomus beckfordi*, female, SL 29.5 mm., SU 50261.

COLOR IN ALCOHOL.—Preserved specimens from Belém, State of Pará, Brazil (figs. 2 and 3) have the following color: Top of head light to dark brown. Primary horizontal stripe extending from tip of snout and tip of lower jaw across maxillary and first orbital bone onto eye. Posterior to eye, primary stripe continuing to posterior edge of opercular bone, but absent or extremely pale on fleshy opercular flap. Beginning on cleithrum and underneath opercular flap, primary horizontal stripe continuing posteriorly over lower midsides onto caudal fin, its course reaching posterior root of anal fin, covering entire lower half of caudal peduncle and continuing onto caudal fin as a wedge with its apex at posterior junction of upper and lower caudal fin lobes. In mature males primary horizontal stripe covering entire fourth horizontal scale row and adjacent parts of third and fifth scale rows. In mature females and immature specimens of both

sexes lower portion of third scale row often only partly pigmented. No evidence of secondary or tertiary horizontal stripes.

Very pale stripe extending above primary horizontal stripe from eye to end of third scale row; this stripe often obscured by light brown color extending ventrally from dorsum. Females, and sometimes males, with scatterings of melanophores forming oblique bands in area of sixth to eighth vertical scale rows and over thirteenth to fifteenth vertical scale rows. Sides pale below primary horizontal stripe, shading to white on belly. Pectoral and pelvic fins translucent but pelvic fins sometimes with scattering of brownish melanophores giving entire fin light brown appearance. Dorsal fin translucent except for fairly dense accumulation of melanophores along anteriodistal portion. Anal fin hyaline except for some accumulation of melanophores in distal region of posteriormost rays.

Color in life.—(The color recorded here is from breeding male aquarium specimens from an unknown locality. These specimens appeared, when preserved, exactly like the specimens described above from Belém.) Dorsal fin, pectoral fins, and pelvic fins mostly hyaline without red except for small amount at base of pelvic fins. Primary horizontal stripe dark bluish black. Narrow silvery blue to golden stripe above primary horizontal stripe, beginning at posterior border of eye and extending to posterior end of caudal peduncle. Above this, beginning between third to sixth vertical scale row, with narrow red stripe, varying in intensity from deep crimson red to pale rose. This red stripe usually absent in nonbreeding males. Intense crimson spot above and below primary horizontal stripe at base of each caudal lobe. Intense red stripe often spreading completely over anal fin below primary horizontal stripe, and usually extending from sixth or seventh vertical scale row posteriorly to above anal fin in breeding males. Nonbreeding males often without red. Distal one-quarter to one-third of pelvic fins intense silvery blue. Some specimens with this color on distal tips of third, fourth, and fifth anal fin rays. Mature females and immature specimens of both sexes often with small amount of silvery blue at distalmost tips of pelvic rays. Dorsum pale brown above silvery and red stripes with each exposed scale edge outlined in darker brown. Lateral surface of snout above primary horizontal stripe pale brown. Top of head brown. Bright metallic-red spot frequently present near anterior narial opening. Iris silvery with reddish suffusion dorsally. Belly and throat regions white.

Remarks.—Hoedeman (1950, pp. 16–18) seems to have been correct in assuming *Nannostomus anomalus* Steindachner to be a synonym of *Nannostomus beckfordi*, a polymorphic species. Hoedeman pointed out that the only difference between *beckfordi* and *anomalus* recorded in the literature is that *beckfordi* has a black spot on the

lower half of the gill cover. Hoedeman noted that at night there is a dark spot on the lower half of the gill cover of living specimens of a fish, apparently without known locality. He considered this fish to be *beckfordi*. These specimens apparently also fit the description of *anomalus*. I have been unable to confirm the presence of such a spot in living specimens available to me. The live specimens I have seen are without locality but are like specimens known to have come from near Belém, Pará, Brazil. Professor George S. Myers kindly examined the holotype of *beckfordi* in the British Museum and noted that the black spot on the lower half of the gill cover is a dirty black smudge, does not consist of melanophores, and occurs on the left side only. Since the spot appears to be an artifact, *anomalus* is here considered a synonym of *beckfordi*.

Meinken (1931) described *Nannostomus aripirangensis* from Aripiranga Island near Belém, Pará, Brazil. Herr Meinken (in litt.) has stated that the types of *aripirangensis* were destroyed during World War II, and no one reexamined them subsequent to Meinken's original account. Hoedeman (1950, p. 118) was possibly correct in assuming *aripirangensis* to be a subspecies of *beckfordi*. I have examined two specimens of *Nannostomus* from Aripiranga Island that were sent to Dr. George S. Myers prior to 1934 by Arthur Rachow, a prominent German aquarist. These specimens are said to be representatives of *aripirangensis* and are identical to specimens of *beckfordi* from around Belém. However, Meinken (1954, and in personal communications) has insisted that *aripirangensis* represents a distinct species. I have seen many living aquarium specimens of *Nannostomus* without locality data which I consider to be color variants (possibly geographical races or subspecies) of *beckfordi*. In appearance, one of these groups of specimens was like specimens of *beckfordi* collected at Belém, Pará, and Aripiranga Island and had, when breeding, some colors suggesting those described for *aripirangensis* by Meinken. Aripiranga Island, the type locality of *aripirangensis*, is just a few miles from the city of Belém, Pará.

Meinken showed in his drawings a small tertiary horizontal stripe, a stripe which I have never seen in any specimens that I could refer to *beckfordi*. Meinken's dorsal fin count of 11 rays should be considered with caution and some doubt, for all *Nannostomus* and *Poecilobrycon* so far examined by me have had a dorsal fin ray count of ii,8 or a total of 10 rays, not 11. Meinken's count may have been taken from an abnormal or rare variant specimen. Meinken has stated in a personal communication that *anomalus* (here *beckfordi*) and *aripirangensis* have interbred in aquaria and that in this manner the living stock of *aripirangensis* has been lost in Germany. This indicates at least a close genetic relationship. Recently Vorderwinkler

(1957), in an aquarium publication, has recorded and published photographs of two forms of *Nannostomus*, one of which is stated to be *anomalus*, the other *aripirangensis;* both of these photographs appear to be of *beckfordi*, showing two of its several geographical color variants. Neither has a color pattern exactly like that described for the original *aripirangensis*.

Until thorough collections of *Nannostomus* can be made on the Island of Aripiranga, the problem of the distinctness of *aripirangensis* cannot be settled; however, I tentatively prefer to consider *aripirangensis* one of the several geographically distinct populations of *beckfordi*.

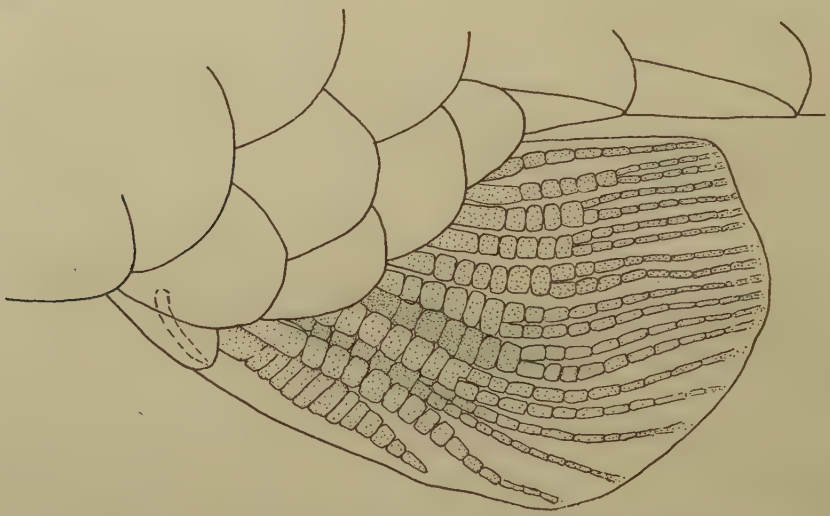

FIGURE 4.—Anal fin of male *Nannostomus beckfordi*, SL 31.0 mm., SU 50261.

Nannostomus beckfordi appears to be a polytypic species with a wide geographical range, known from the Guianas and for a considerable distance (about 700 or more air miles) up the Amazon River. Adequate collections and studies will undoubtedly show that this species consists of several distinct populations, some of which may prove to be subspecies. Studies of color variation, variation in certain body proportions (especially head depth compared to body length and caudal peduncle length), vertebral counts, and arrangement of tooth cusps will probably be of great value in studying subspecific population differences.

SPECIMENS EXAMINED.—Three, SU 50256, SL 22.0–22.7 mm., Brazil, State of Pará, Belém, May 18, 1924, Carl Ternetz.—Four, SU 50262, SL 22.5–27.5 mm., Brazil, State of Pará, brook into Tápajos near Santarém, Aug. 2, 1924, Carl Ternetz.—Forty-four, SU 50257, SL 16.0–29.0 mm., Brazil, State of Pará, south

bank of Rio Amazonas, Rio Uruará, about lat. 1°54′ S. and long. 53°27′ W., June 26, 1924, Carl Ternetz.—Six, SU 50258, SL 22.0–26.5 mm., alizarin preparations, Brazil, State of Pará, south bank of Rio Amazonas, Rio Uruará about lat. 1°54′ S. and long. 53°27′ W., June 26, 1924, Carl Ternetz (from SU 50257).—Five, SU 50261, SL 20.5–29.6 mm., Brazil, State of Pará, Belém (Utinga Forest Reserve), September 1944, George S. Myers.—Two, SU 18469, SL 20.5–22.5 mm., no locality, aquarium specimens sent to Dr. George S. Myers as specimens of *Nannostomus aripirangensis*.—Two, USNM 94207, SL 30.0–31.0 mm., Brazil, state of Pará, Aripiranga Island, sent to Dr. George S. Myers prior to 1934 by Arthur Rachow.—Four, SU 50269, SL 19.0–25.0 mm., Brazil, State of Pará, Igarapé Uruará, tributary of Furo Maicá, about 10 miles southeast of Santarém, about lat. 2°30–55′ S. and long. 54°35–41′ W., June 23, 1924, Carl Ternetz.—Two, SU 50260, SL 25.0 mm. (both specimens), Brazil, State of Pará, Lagôa do Maicá, at the junction of the Igarapé Maicá and the Furo do Ituquí, about lat. 2°27′ S. and long. 54°40′ W., Apr. 2, 1924, Carl Ternetz.—Three, SU 50255, SL 22.0–24.0 mm., Brazil, State of Pará, Santarém, brook into Rio Tápajos, June 30, 1924, Carl Ternetz.—Nine, SU 50259, SL 21.0–25.4 mm., French Guiana, Baduel, on the Île de Cayenne, July 26, 1947.—Forty-three, CM 19648, SL 20.0–27.0 mm., Brazil, State of Pará, Obidos, 1856, Col. Bentos, Thayer Expedition.—One, CAS (IUM) 11692, SL 20.3 mm., paratype of *Nannostomus simplex*, British Guiana, Lama Stop-Off, Mahaica River, 1908, Carl H. Eigenmann.

Nannostomus bifasciatus Hoedeman

Nannostomus bifasciatus Hoedeman, 1953, p. x30.11.311 (original description, in Dutch; type locality: Berg en Dal at Surinam River, Surinam; holotype in Amsterdam Museum); 1954a, p. 85 (description in English); 1954b, p. 77 (description from life).—Sterba and Tucker, 1962, p. 211 (description and aquarium notes).

Diagnosis.—At least a few perforated lateral-line scales present; about 8+14 gill rakers; iii,9 anal fin rays, secondary horizontal stripe present, scales in a lateral series about 25.

Note.—This species is known from only four specimens and the original author has kindly sent three of them for examination. The fish was an aquarium import from Surinam to the Netherlands and the three available specimens are in poor condition, two having been dried at one time and all with torn, broken fins and broken jaws with missing teeth. Unfortunately the original description was inadequate and inaccurate, and it is impossible completely and competently to describe or illustrate the fish from the specimens at hand.

Description.—Body elongate; sides somewhat flattened and body compressed posteriorly. Greatest depth just anterior to origin of dorsal fin. Standard length of longest specimen examined 28.3 mm. Greatest body depth 5.4 (5.3–5.6) [females with ripe eggs not at hand but undoubtedly deeper bodied (see illustrations of live specimens in Hoedeman 1954a and Nieuwenhuizen 1954)]; least depth of caudal peduncle 11.6 (11.4–11.9); length of caudal peduncle 5.6 (5.5–5.6) in females, male damaged. Snout tip to origin of dorsal fin 1.9 (1.9–1.9); snout tip to origin of anal fin 1.3 (1.3–1.3).

Head conic and snout obtuse in both vertical and horizontal profiles, top of head gently convex between eyes. Head 3.8 (3.8–3.8); eye in head 3.1 (3.0–3.2); snout in eye 1.3 (1.2–1.3); least width of long interorbital in greatest eye diameter 1.3 (1.3–1.3).

Premaxillary with 7 teeth; anterior and lateral teeth septemcuspid, third from anterior or median cusp largest. Maxillary with 1 quadricuspid tooth. Dentary with 6 teeth, each usually with 7 cusps. Third cusp from medial or anterior end of tooth largest; sometimes central cusp largest. Inner row of teeth damaged in all specimens but appears to be over 10 simple conic teeth. Gill rakers 8+14 (one alizarin, specimen).

Dorsal fin ii,8; anal fin iii,9. Adipose fin absent. Caudal fin with principal rays 10/9.

Anal fin of male in good condition, somewhat modified. First ray small and completely hidden by a basal scale. Second ray enlarged and its anterior edge expanded and carinate. Entire fin larger than that of females and individual rays thickened laterally and somewhat enlarged in an anterior and posterior plane. In folded position, rays take an alternate position to each other with regard to median plane. However, anal fin not nearly as modified as that of *Nannostomus digrammus*.

Radial grooves of scales belonging to that part of third horizontal scale row below dorsal fin having posterior field with 1 to 3, usually 2 radial grooves; dorsal and ventral fields with 1 and anterior field with 3 to usually 4 radial grooves. Scales in lateral series 25 in single countable specimen. This specimen also with 3 perforated lateral-line scales in single row behind cleithrum. Scales in a median series before dorsal fin 10 in 2 female specimens. Total number of vertebrae 36 (19 precaudal and 17 caudal).

Color in alcohol.—Top of head and back light brown. Dorsum at base of dorsal fin dark brown. Primary horizontal stripe dark brown, extending from snout tip and lower jaw onto anterior surface of eye, across lower border of fifth orbital bone and upper border of fourth orbital bone to over upper limb of preopercle, finally terminating at posterior border of bony opercle. On body, primary horizontal stripe beginning anteriorly underneath fleshy opercular flap and extending through middle of fourth scale row, covering lower and upper exposed portions of third and fifth scale rows respectively. Primary stripe widening posteriorly until over anal fin covering entire fourth scale row and upper half of fifth scale row. Primary horizontal stripe covering entire lower half of caudal peduncle and entering lower lobe of caudal fin. Its pattern over lower lobe of caudal fin could not be determined due to damage. Below primary horizontal stripe, sides and belly pale brown (probably silvery in

well-preserved specimens) with few irregularly scattered melanophores. No evidence of tertiary stripe. Single broad pale brown stripe (probably silvery in well-preserved specimens) above primary horizontal stripe extending from eye to caudal fin base. Two areas of large scattered melanophores occurring on pale stripe, forming oblique bands; anterior band covering 4 scales anterior to a point below anterior origin of dorsal fin, posterior band covering another 4 scales and center of this area located at a point dorsal to vent. Just dorsal to pale stripe a narrow secondary stripe arising a short distance above termination of upper opercular opening and extending posteriorly through center of second scale row to below dorsal fin, here becoming wider, denser, and rising to top of second scale row, there merging with dark pigment of dorsum behind dorsal fin and above pale stripe on caudal peduncle. Dorsum anterior to dorsal fin pale brown, lighter than secondary stripe. Top of head and snout with scattered large and small melanophores forming an area darker than dorsum just anterior to dorsal fin. All fins colorless except for a few scattered melanophores and dark pigment on lower caudal lobe. Pelvic fins appear artificially stained gray.

Color in life.—Life colors are taken from the original English description. Primary horizontal stripe "brilliant" black, extending onto caudal fin rays and onto lower caudal lobe. Typical wedge-shape distribution of pigment on lower caudal fin lobe apparently not present but precise distribution of black pigment not stated. Dorsal and ventral region dusky, back darker. Faint "reddish flush" on base of caudal and anal fins. Pelvic tipped with "ice blue," especially in males. Sides above and below primary horizontal stripe white except for narrow "golden-red streak" above primary stripe. (Hoedeman stated that this streak is diffuse at times except on snout. From this I would assume that there is probably a golden or red metallic spot at the anterior narial openings as in so many other nannostominans.) Secondary horizontal stripe present but tertiary stripe absent.

Remarks.—Concerning his new species, *N. bifasciatus*, Hoedeman (1954a) stated: "Phylogenetically the new species seems close to the stem of the tribe [i.e., his tribe Nannostomidi], near the presumed Pre-Nannostomid, taking an intermediate position between *Nannostomus beckfordi* and *Nannobrycon eques*." Hoedeman's opinion was apparently based on the following observation: "The oblique swimming position of *Nannobrycon* though less pronounced is sometimes observed in the present species [*bifasciatus*] also, especially while nipping planktonic food from the plants." He also mentioned that the black pigment of the caudal fin extends on the lower caudal fin lobe somewhat as in *Poecilobrycon eques* and remarked that the

adipose fin of *bifasciatus* is placed more like that of members of *Nannostomus* than that of *Poecilobrycon harrisoni*, which has the adipose fin posterior to the anal fin, not over it as in *Nannostomus*. Hoedeman remarked that *bifasciatus* has a vestigal adipose fin; however, I find no trace of one in his 3 specimens. In addition I fail to find any generic significance in the placement of the adipose fin in nannostominans. It is somewhat more posterior in *Nannostomus trifasciatus* and *Poecilobrycon harrisoni* but more anteriorly placed in all other species of nannostominans which possess this fin. Concerning the swimming position, I can make little comment because I have not seen living specimens of *bifasciatus*. However, it should be remarked that *Poecilobrycon harrisoni* normally swims horizontally like all living species of *Nannostomus* that I have seen and that all species of *Nannostomus* will occasionally swim slightly obliquely when feeding. The color claimed for the caudal fin may be like that of *Poecilobrycon eques*, but I cannot determine this from the specimens at hand. The precise significance of this color pattern if present would be difficult to determine. From the key in the present paper it would seem that *bifasciatus* is closest to *beckfordi* in several characters and in fact may be rather closely related to it. I fail to find that Hoedeman presented sufficient evidence to indicate either that *bifasciatus* is a relatively primitive nannostominan or that it is intermediate between *Nannostomus* and *Nannobrycon*. The osteology of *bifasciatus* is typically that of *Nannostomus*. Weitzman (1964) noted that pyrrhulininans and nannostominans undoubtedly had a common ancestor. Presumably a relatively primitive nannostominan would have some characters suggesting pyrrhulininans. The only nannostominan that does this is *Nannostomus espei*, and even in this species the few such characters are difficult to evaluate.

SPECIMENS EXAMINED.—Three, paratypes, AM 100513, SL 27.2–28.3 mm. (only 2 specimens could be measured as snout of 1 damaged), Surinam, Berg en Dal at Surinam River.

Nannostomus digrammus Fowler

FIGURES 5, 6

Nannostomus digrammus Fowler, 1913, p. 525 (original description; type locality: Rio Madeira, about 200 miles east of long. 62°20′ W., Brazil;[2] holotype in Academy of Natural Sciences of Philadelphia), 1950, p. 261 (listed).

Poecilobrycon diagrammus.—Hoedeman, 1954a, p. 84 (copied description).

Poecilobrycon digrammus.—Hoedeman, 1954b, p. 71 (listed).

Nannostomus beckfordi beckfordi.—Sterba and Tucker (not Günther), 1962, p. 209, (aquarium description of "gold anomalus" but counts from Günther's original description of *beckfordi;* see remarks below).

[2] Bohlke (1955, pp. 8–12) doubts the quoted locality and presents reasons why it may be considered as being 20 miles east of long. 62°20′ W.

Diagnosis.—This species may be distinguished from all other known species of *Nannostomus* and *Poecilobrycon* by the greatly modified anal fin of the males (fig. 6) and an anal fin count of iii,8 in both sexes. In addition, the following combination of characters will distinguish this species from all others: Primary and secondary horizontal stripes well developed; tertiary horizontal stripe absent or only weakly developed; no perforated lateral-line scales; and adipose fin present.

Description.—Body elongate, rather cylindrical in its anterior half but compressed posteriorly. Greatest depth a short distance anterior to origin of dorsal fin. Standard length of largest specimen with locality data 25.0 mm. (an aquarium specimen measured, SU 18471, SL 27.6 mm.). Greatest body depth 4.7 (4.5–5.0); least depth of caudal peduncle 11.1 (10.3–11.5); length of caudal peduncle, males 5.9 (5.6–6.3), females 5.1 (4.9–5.4); snout tip to origin of dorsal fin 1.8 (1.7–1.9); snout tip to origin of anal fin 1.3 (1.29–1.34).

Figure 5.—*Nannostomus digrammus*, male, SL 24.5 mm., SU 50248.

Head conic but somewhat flattened dorsoventrally; snout obtuse in vertical and horizontal profiles. Top of head between eyes rather convex. Head 3.7 (3.5–3.8); eye in head 2.8 (2.5–3.0); snout in eye 1.2 (1.1–1.3); least width of bony interorbital in greatest eye diameter 1.2 (1.05–1.26).

Premaxillary with 6 teeth in anterior row, all quadricuspid; posterior 1 or 2 teeth of this row quinque- to sexcuspid, cusps being subequal. Central cusps of each tooth largest and longest. Maxillary with 1 quinque- to sexcuspid tooth. Dentary with 5 to 6 (usually 6) teeth in outer row, anterior 4 teeth with 6 cusps, posterior 2 teeth with 4 to 5 cusps, cusps subequal. Teeth in inner or second tooth row of

dentary 1 to 4 in the alizarin specimens. Gill rakers 7+14 (alizarin specimens).

Dorsal fin ii,8; anal fin iii,8; pectoral i,8 to i,10; pelvics ii,7. Adipose fin present on all specimens, its base above scale row that runs diagonally to posterior base of anal fin. Caudal fin with principal rays 10/9. Distal tips of all elements of first 10 rays contained in upper caudal lobe. Lower lobe containing all distal tips of remaining 9 principal rays.

Highly modified anal fin of male *Nannostomus digrammus* (fig. 6) with an interesting structure. Unbranched anterior rays 3, followed by 7 once dichotomus branched rays; terminal or last ray unbranched. Last ray not divided to its base and with its own separate pterygiophore, or radial series. Except for anteriormost small ray hidden below scale at anterior base of anal fin, each of first 6 rays greatly expanded anteriorly and posteriorly. These rays arranged as follows in collapsed fin: Second ray (first large ray of anal fin) partially enclosed by anterior edges of ray halves of third anal ray. Thus appressed posterior borders of ray halves of second ray enclosed by 2 diverging anterior borders of third anal fin ray. Anterior edge of fourth anal ray (including both ray halves) lying to left of posterior border of third anal ray. Anterior border of fifth anal ray lying to right of posterior border of third anal ray and to right of entire middle region of fourth anal ray. Sixth anal ray lying to left of posterior border of fifth ray and will even slip to left of posterior border of fourth ray. Anterior edge of seventh anal ray lying to right of posterior half of sixth anal ray and posterior border of seventh ray lying to right of anterior border of eighth ray. Anterior border of ninth ray lying to right of posterior border of eighth ray, but tenth and eleventh rays with usual position in being just posterior to rays anterior to them. Fourth ray with its left lateral face convex, its right lateral face concave. Fifth ray, converse of fourth, and sixth ray with convex and concave faces facing same sides as fourth ray. This alternation continuing to eighth ray. Ninth through eleventh anal rays with little if any convexity or concavity.

Inclinator muscles extending bilaterally ventrally far beyond base of anal fin rays and inserting on lepidotrichs to about one-half length of tenth and eleventh anal fin rays. Similarly inclinator muscle extending ventrally beyond scales and inserting along basal one-fifth of second anal fin ray (fig. 6).

Many male nannostominans and some male pyrrhulininans have anal fins that are modified in a manner similar to that noted here for *Nannostomus digrammus*. However, none have their anal fin rays modified as greatly as those of *digrammus*. Species of nannostominans and pyrrhulininans that I have seen breeding in aquaria all have been

capable, to a greater or lesser degree, of twisting the anal fin into a cup-shaped organ that is placed with the concave side almost over the female's vent during the act of laying an egg. Wickler (1957) has recorded some of the behavior of various species of nannostominans but has not noted the precise use of the anal fins. Although I have not seen the anal fin of the male *Nannostomus digrammus* in use, its morphology indicates that it undoubtedly changes greatly in shape during the spawning act.

FIGURE 6.—Anal fin of male *Nannostomus digrammus*, SL 19.6 mm., SU 50251.

Radial grooves of scales belonging to third horizontal scale series and lying below dorsal fin shown in figure 5. Posterior field with 1 or 2 radial grooves; dorsal and ventral fields each with 1 and anterior field with 3 or 4 radial grooves. Scales in lateral series 25 to 26; no perforated lateral-line scales; scales in median series anterior to dorsal fin 10 to 11. Total number of vertebrae 34 to 35, 18 to 19 precaudals and 15 to 16 caudals, but always in a combination to produce a total count of 34 to 35 vertebrae.

COLOR IN ALCOHOL.—Top of head black. Primary horizontal stripe black, extending from snout tip and lower jaw onto anterior surface of eye, then from posterior surface of eye across lower border of fifth orbital bone and upper border of fourth orbital, then continuing over upper arm of preopercle onto opercle ending at about posterior bony

border of opercle. On body, primary horizontal stripe begins anteriorly underneath fleshy opercular flap and extends through approximately lower half of fourth scale row and upper third of fifth scale row. Primary stripe widening posteriorly until, over anal fin, there covering entire fourth, and one-half of fifth scale rows. Posterior to this, primary horizontal stripe covering almost entire lower half of caudal peduncle and continuing as an acute wedge posteriorly over caudal fin, ending at base of caudal fork. Below primary horizontal stripe, sides and belly silvery with few irregularly scattered melanophores. Broad silvery stirpe extending from eye to caudal base above primary horizontal stripe. Silvery stripe with oblique band, about 3 scales long, located just anterior to dorsal fin. This area spotted with large, dark melanophores. Few small melanophores scattered over entire silvery stripe. Narrow, dark secondary horizontal stripe just dorsal to silvery lateral stripe, beginning at upper posterior edge of operculum and ending on upper part of caudal peduncle posterior to adipose fin. Dorsum pale brown above secondary horizontal stripe. Areas of head and eye not covered by dense black pigment, silvery with few scattered melanophores. Dorsal, pelvic, pectoral, and anal fins colorless. Caudal fin, in addition to having narrow wedge of primary horizontal stripe, with fairly dense aggregation of melanophores along first 3 upper principal rays of upper lobe. Some melanophores scattered over entire fin. Color in life not known with certainty.

Remarks.—*Nannostomus digrammus* was known previously only from the four specimens reported in the original description. However, this species has been imported as an aquarium fish. Several years ago a prominent aquarist, Mr. Frederick Stoye, sent a specimen of a nannostominan to Dr. George S. Myers at Stanford University. This specimen, labeled as the "gold anomalus," proved to be a large male *digrammus*.

All the specimens belonging to the original type lot of *digrammus* were females, and the holotype illustrated by Fowler shows the anal fin of a female.

Sterba and Tucker (1963, p. 209) believed the so-called "gold anomalus" to be Günther's original *Nannostomus beckfordi*. However Stoye's specimen mentioned above would seem to show that the "gold anomalus" of aquarists is *N. digrammus*. Aquarists' records of this fish cited by Sterba and Tucker (1963) are difficult to compare. Perhaps more than one species of fish is involved. However, live specimens of *Nannostomus beckfordi* from British Guiana are comparatively pale in color, never exhibiting the colors described for the "gold anomalus."

Specimens examined.—Two, paratypes, ANSP 39190 and 39191 SL 18.0–19.0 mm., Brazil, State of Amazonas, Rio Madiera, about 200 miles east of long.

62°20′ W., September 1912, Edgar A. Smith.—Eleven, MCA 19797, plus 2 alizarin specimens SU 50249, SL 16.3–19.4 mm., Brazil, State of Amazonas, Manáos, 1865, Louis Agassiz.—Two (male figured), SU 50248, SL 24.1–24.5 mm., Brazil, Pará, Igarapé do Sapucuá into Lagôa Sapucuá (This lake drains into the Rio Trombetas. The Trombetas flows into the Amazon from the north about 25 miles west of Obidos.), June 7, 1924, Carl Ternetz.—Fifteen, SU 50250, three alizarin preparations SU 50251, SL 18.0–22.8 mm., Brazil, State of Amazonas, Igrapé do Mãi Joana, a tributary of the Rio Negro near Manáos, Dec. 25, 1924, Carl Ternetz.—One, SU 18471, SL 27.6 mm., (a large adult male), an aquarium specimen sent to Dr. George S. Myers by Mr. Frederick Stoye.—Eight, SU 51024, SL 14.8–16.0 mm., British Guiana, Rupununi District, Nappi River, Rio Branco drainage, about lat. 30°30′ N., long. 59°32′ W., Sept. 29, 1957, Rosemary Lowe (McConnell).—One, SU 51025, SL 15.5 mm., British Guiana, Manawarin River, a tributary of the Moruka River about lat. 7°30′ N., long. 59°11′ W., July 16, 1957, Rosemary Lowe (McConnell).—One, SU 51026, SL 16.0 mm., British Guiana, Kumarow Creek pool into the Rupununi River, a tributary of the Essequibo River, Dec. 10, 1957, Rosemary Lowe (McConnell).—One, SU 50448, SL 17.2 mm., British Guiana, pool near Takatu River, Rio Branco drainage, Emprensa, Rupununi District, Dec. 8, 1957, Rosemary Lowe (McConnell).—One, SU 50450, SL 19.5 mm., British Guiana, Kumarow Creek Pool which flows into the Rupununi River in southern savannas of the Essequibo River Drainage, Dec. 10, 1957, Rosemary Lowe (McConnell).

Nannostomus trifasciatus Steindachner

FIGURE 7

Nannostomus trifasciatus Steindachner, 1876, p. 123, pl. 9, fig. 2 (original description; localities: backwaters and quiet tributaries of the Amazon close to mouth of the Rio Negro, Brazil; also Amazon at Tabatinga; types in Vienna museum).—Eigenmann and Eigenmann, 1891, p. 49 (listed).—Eigenmann, 1910, p. 427 (listed).—Innes, 1935, p. 155 (description from life and photograph) and later editions.—Hoedeman, 1950, p. 18 (description).—Axelrod and Schultz, 1955, p. 248 (description, aquarium notes).—Sterba and Tucker, 1962, p. 212 (description and aquarium notes).

?*Cyprinodon amazona* Eigenmann, 1894, p. 627 (in part; original description; type locality: Lower Amazonas; types apparently lost).—Garman, 1895, p. 28 (in part; copied description).—Hubbs, 1926, p. 16 (in part; discussion of identity).—Fowler, 1954, p. 216 (in part; listed).

Poecilobrycon erythrurus Eigenmann, 1909, p. 44 (original description; type locality: Rockstone, British Guiana; holotype in Chicago Natural History Museum).—Eigenmann, 1910, p. 427 (listed).—Eigenmann, 1912, p. 285, pl. 37, fig. 3 (description).

?*Cyprinodon amazonus* Eigenmann, 1910, p. 456 (in part; listed).

Poecilobrycon vittatus Ahl, 1933, p. 84, fig. (original description; type locality: "Pará"; type presumably in Berlin Museum); 1934, p. 124 (a longer, more useful description; no figure).

Nannostomus trilineatus (lapsus for *trifasciatus*) Innes, 1933, p. 142 (description from life).—Ladiges, 1948, p. 30 (description from life).

NOMENCLATURAL NOTE—The identity of *Cyprinodon amazona* is in doubt, but it seems most likely the fish is a synonym of either *Nannostomus trifasciatus* or *Nannostomus marginatus*. Eigenmann de-

scribed the fish from 18 specimens collected by Frederick C. Hartt somewhere along the "Lower Amazon." Hubbs (1926), after examining the specimens, reported that the fish belongs to the genus *Nannostomus* and at that time Eigenmann, in personal communication with Hubbs, concurred in this referral. Neither Hubbs, Eigenmann, nor anyone else has tried to identify Eigenmann's syntypes of *amazona* with any known species of *Nannostomus*. Unfortunately, a check of various American museums and with Dr. Hubbs has not located the type specimens. From examination of Eigenmann's original description it seems probable that two species, *Nannostomus marginatus* and *N. trifasciatus*, were among the original specimens. Measurements and counts include the range of both species, and the color description could be of either species. It seems likely that the male mentioned by Eigenmann is *N. marginatus* but that some of the other specimens are most probably *N. trifasciatus*. The name *trifasciatus* Steindachner 1876 predates *amazona* Eigenmann 1894; however, *amazona* predates *marginatus* Eigenmann 1909; *Nannostomus marginatus* is a well-established name, especially in the aquarium literature, where it is used frequently. It would serve no useful purpose to substitute the name *amazonus* for *marginatus*, especially since some of the syntypes at least appear to have been *trifasciatus*. If the types of *amazona* are ever found and some of them prove to be *trifasciatus*, one of these should be selected as the lectotype and *Cyprinodon amazona* placed in the synonymy of *Nannostomus trifasciatus*.

Diagnosis.—This species, like *Nannostomus beckfordi*, lacks obvious unique characters, but it may be readily diagnosed by the following combination of characters: Anal fin rays completely unmodified; gill rakers 9+13; scales in a lateral series 26–27; perforated lateral-line scales 3 to 5; one maxillary tooth present; primary, secondary, and tertiary horizontal stripes present; 11 teeth in second tooth row of dentary.

Description.—Body elongate, somewhat cylindrical through anterior half, but sides flattened and body compressed posteriorly. Greatest depth lying between posterior tip of appressed pectorals and origin of dorsal fin. Standard length of largest specimen 28.2 mm. (a larger aquarium specimen, a male, measured at 32.5 mm.). Greatest body depth 4.6 (4.5–4.7); least depth of caudal peduncle 10.2 (10.0–10.4); length of caudal peduncle (including both sexes) 5.8 (5.6–6.1); snout tip to origin of dorsal 1.9 (1.8–2.0); snout tip to origin of anal 1.28 (1.27–1.30).

Head elongate, rather depressed, especially in snout region; top of head only slightly convex between eyes. Snout obtuse, especially so in dorsal profile. Head 3.6 (3.4–3.9) [Peruvian specimens 3.7–3.9,

British Guiana specimens 3.4–3.6]; eye in head 3.0 (2.9–3.1); snout in eye 1.0 in all specimens examined; least width of bony interorbital in greatest eye diameter 1.0 in all specimens.

Premaxillary with 7 quinquecuspid teeth, lateroposterior cusp largest. Maxillary having 1 tooth with 4 or 5 cusps. Dentary with 8 sexcuspid teeth, cusps subequal and central cusps longest; 11 teeth in second row of dentary in alizarin specimens. Gill rakers 9+13.

Dorsal fin rays ii,8; anal iii,9; pectoral i,9 to i,10; pelvics iii,7. Adipose fin present in all specimens examined but reduced in size in some. Caudal fin with principal rays 10/9; distal tips of all elements of first 10 principal rays in upper caudal lobe. Lower caudal lobe with all elements of remaining 9 principal rays.

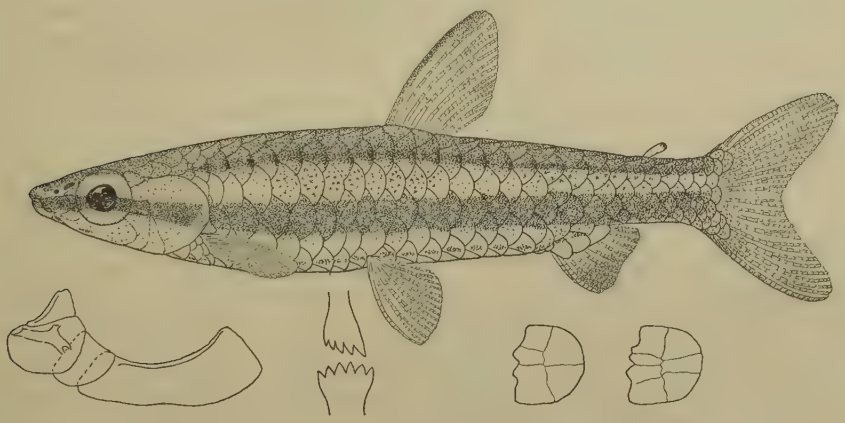

FIGURE 7.—*Nannostomus trifasciatus*, male, SL 27.5 mm., SU 36899.

Anal fins of male and female appear alike in this species; rays of male's anal fin not modified. Inclinator muscles appear slightly, if at all, more developed in male than in female.

Radial grooves of scales belonging to third horizontal scale series and lying below dorsal fin are shown in figure 7. Posterior field with 1 or 2 radial grooves. Dorsal and ventral fields each with 1 radial groove and anterior field with 2 to 4 radial grooves. Scales in a lateral series 26 to 27; 3 to 5 lateral-line scales and 10 scales in median series anterior to dorsal fin. Total number of vertebrae 35 to 36, 19 precaudal and 16 or 17 caudal vertebrae.

COLOR IN ALCOHOL.—Top of head light to dark brown. Primary horizontal stripe extending on head from snout tip and lower jaw posteriorly over first orbital bone across eye and operculum, terminating at posterior border of operculum. On body, primary horizontal stripe extending from under fleshy flap of opercle through fourth scale

row and partially on adjoining third and fifth scale rows; expanding over anal fin to include one-half of third scale row and on caudal peduncle extending downward to all but the lowermost vertical scale row. Primary horizontal stripe ending on caudal peduncle in Peruvian specimens but extending posteriorly onto caudal fin as a very narrow wedge on most specimens from British Guiana.

Above primary horizontal stripe, pale stripe extending from eye to caudal peduncle. Melanophores scattered over entire surface of this stripe being thicker and heavier in region of fifth through eleventh and sixteenth to twentieth vertical scale rows. These areas constitute oblique bands. Secondary horizontal stripe dorsal to silvery lateral stripe, and extending from posterior upper end of gill cover through second row of scales onto caudal peduncle. Secondary horizontal stripe darker and wider at posterior margin of each scale in second row. Back above secondary horizontal stripe dark, rather densely covered with melanophores. Sides below primary horizontal stripe lightcolored with few scattered melanophores. On sixth scale row tertiary horizontal stripe extending from below operculum along sides of belly, where extending over or interrupted by pelvic fins, and then continuing to posterior end of base of anal fin. Tertiary horizontal stripe narrow and sometimes absent or restricted to region behind pelvic fins. Portion of tertiary horizontal stripe on head along surface of third orbital bone. Pectoral and pelvic fins without dense aggregations of melanophores. Sometimes rather weak aggregation of melanophores present along uppermost and lowermost principal caudal fin rays. Dorsal fin dusky on its anterior distal portion and first and second unbranched rays frequently dark. Anal fin of male and sometimes female dusky along its distal and anterior regions. Sometimes this duskiness not evident.

Color in life.—The color description given below agrees well with that given by Eigenmann (1909, p. 45) for live specimens of *Poecilobrycon erythrurus* from British Guiana. The specimens used here were collected in British Guiana by Louis Chung in 1955 or 1956 but are without definite locality. Midanterior region of dorsal fin with single bright red spot. Red spots on base of upper and lower lobes of caudal fins and bright red spots on anterior base of anal fin and proximal region of pelvic fin. In some specimens these red spots almost absent. Location of these spots well shown in color photograph by Innes (1953, p. 192). Photograph in Axelrod and Schultz (1955, p. 248) shows color of this species well. Primary horizontal stripe metallic pale green-gold. Caudal fin posterior to metallic pale green-gold stripe with few streaks of white pigment. Thin red line extending lengthwise through center of metallic pale green-gold stripe. Frequently this red line broken into series of streaks, reduced in length or

absent. Laterodorsal and anterior surface of snout anterior to nostrils bright red. Also single red line in upper part of iris. Remainder of iris pale gold except where primary horizontal stripe extends through eye. Distal region of pelvics silvery blue, especially in male. In some specimens this color almost absent. Belly and region below primary horizontal stripe silvery white.

REMARKS.—*Poecilobrycon vittatus* of Ahl (1933) was described very poorly and the type locality is indefinite. Ahl, following Eigenmann, seemed confused about the identity of Steindachner's *trifasciatus* and *eques*, even though, for their time, Steindachner's figures and descriptions of these two species were excellent. Ahl believed his *vittatus* was related to Eigenmann's *erythrurus*, a form which perhaps could be recognized at most as a subspecies of *trifasciatus*. For the most part, Ahl's description of *vittatus* seems to fit the characters listed here for *trifasciatus*, and I concur with Hoedeman (1954) in considering *vittatus* a synonym of *trifasciatus*.

Eigenmann (1909, pp. 44–45) described *Poecilobrycon erythrurus* and noted that it was most closely allied to his own *P. marginatus* (now considered to be *Nannostomus marginatus*) and Steindachner's *P. trifasciatus*. Later Eigenmann (1912, p. 284) considered *Poecilobrycon auratus* to be synonymous with Steindachner's *Nannostomus trifasciatus*. He apparently had mentally transposed Steindachner's *trifasciatus* and *eques*. This probably caused Eigenmann to consider that his *erythrurus* (at most a subspecies of *trifasciatus*) was not *trifasciatus* and therefore that it was a distinct species. In any event, examination of some of Eigenmann's specimens of *erythrurus* and of specimens of *trifasciatus* from near the type locality of the latter indicates that the two forms are closely related and can be considered members of a widespread, somewhat polymorphic species. Adequate study of many samples from populations throughout the range of the species probably will show that there are several distinct races, some of which undoubtedly will be considered as subspecies. Schultz in Axelrod and Schultz (1955, p. 248) considered *Poecilobrycon auratus* Eigenmann a synonym of *Nannostomus trifasciatus*. Examination of type specimens of *auratus* shows it to be a synonym of *Poecilobrycon eques* (Steindachner) (p. 50).

SPECIMENS EXAMINED.—Three, SU 36900 (SL 24.5 mm.), SU 36999 (SL 27.0 mm.), SU 50221 (SL 27.0 mm.), Peru, Shansho Cano, Pévas [Pébas] District, July 28, Oct. 20, 1936 (date for third specimen unknown), W. G. Scherer.—One, SU 50222, SL 33.0 mm., Peru, Río Ampiyacu, Pévas [Pébas] District, July 23, 1944, W. G. Scherer.—Two (paratypes of *Poecilobrycon erythrurus* Eigenmann), CNHM 52974, SL 26.5–28.2 mm., British Guiana, Rockstone River, 1908, Carl H. Eigenmann.—Two (paratypes of *P. erythrurus*), CAS(IUM) 11693, SL 23.0–28.6 mm., British Guiana, Rockstone sandbank, Essequibo River, 1908, Carl H. Eigenmann.—One (paratype of *P. erythrurus*), CAS(IUM) 11694, SL 24.0 mm., British

Guiana, Gluck Island, Essequibo River, 1908, Carl H. Eigenmann.—One (paratype of *P. erythrurus*), CAS(IUM) 11695, SL 25.5 mm., British Guiana, Rupununi River, Twoca Pan, 1908, Carl H. Eigenmann.—One, CNHM 50162, SL 27.0 mm., British Guiana, Rockstone, Essequibo River, Mar. 1937, E. R. Blake.—Five, SU 50223 (one alizarin preparation), SL 25.0–30.0 mm., British Guiana, no other data.—Two, SU 18472 (one alizarin preparation), SL 31.5–32.0 mm., aquarium specimens said to be from "the Amazon," sent to Dr. G. S. Myers by Frederick Stoye, no other data.—Seven, SU 50220, SL 29.5–32.5 mm., aquarium specimens probably from British Guiana, 1955.—Two, SU 50434, SL 21.0–22.1 mm., British Guiana, Moreby Creek, Rupununi River near Karanambo, Essequibo drainage, Sept. 17, 1957, Rosemary Lowe (McConnell).—Two, SU 50437, SL 23.2–24.8 mm., British Guiana, Karanambo, "Grass Pond," Rupununi River, Essequibo drainage, Sept. 14, 1957, Rosemary Lowe (McConnell).—Two, SU 50432, SL 24.0–26.0 mm., British Guiana, "Crane Pond Creek," Karanambo Rupununi River, Essequibo drainage, Sept. 14, 1957, Rosemary Lowe (McConnell).—Two, SU 50440, SL 19.0–27.0 mm., British Guiana, Rupununi District, Nappi River and other Tocatú drainage creeks, Rio Branco drainage, Sept. 20, 1957, Rosemary Lowe (McConnell).

Nannostomus marginatus Eigenmann

FIGURE 8

?*Cyprinodon amazona* Eigenmann, 1894, p. 627 (in part; original description; type locality: Lower Amazonas; types apparently lost).—Garman, 1895, p. 28 (in part; copied description).—Hubbs, 1926, p. 16 (in part; discussion of identity).—Fowler, 1954, p. 216 (in part; listed).

Nannostomus marginatus Eigenmann, 1909, p. 41 (original description; type locality: British Guiana, Maduni Creek, Mahaica River; holotype in Chicago Natural History Museum).—Eigenmann, 1910, p. 427 (listed); 1912, p. 281, pl. 37, fig. 4 (description).—Innes, 1935, p. 154 (description from life and photograph; see also later editions).—Hoedeman, 1950, p. 20 (description; figures).—Boeseman, 1952, p. 184 (Surinam); 1953, p. 16 (Surinam); 1954, p. 18 (Surinam).—Axelrod and Schultz, 1955, p. 241 (description and aquarium notes).—Sterba and Tucker, 1963, p. 211 (description and aquarium notes).

?*Cyprinodon amazonus* Eigenmann, 1910, p. 456 (in part; listed).

Nannostomus marginatus picturatus Hoedeman, 1954a, p. 87 (original description; type locality: "A ditch near Zonderij II, Surinam"; types in Amsterdam Museum).

DIAGNOSIS.—This species is the deepest bodied of all nannostominans; only egg-filled females of *Nannostomus beckfordi* were found to have a body depth as great as the most slender specimens of *marginatus*. The body depth of *marginatus* is 3.5 to 4.0. Their caudal peduncle is the deepest of all nannostominans, 7.5 to 8.5 in standard length. In addition, *marginatus* may be distinguished from all other nannostominans by the following combination of characters: Primary, secondary, and tertiary horizontal stripes all present; maxillary tooth rarely present; 21 to 23 scales in a lateral series; 7+12 gill rakers; 31 to 33 vertebrae; male anal fin with unmodified fin rays.

DESCRIPTION.—Body elongate, robust; sides flattened and body

compressed posteriorly. Greatest depth between posterior tip of appressed pectorals and anterior base of dorsal fin. Standard length of largest specimen examined 25.5 mm. Greatest body depth 3.8 (3.5–4.0); least depth of caudal peduncle 8.0 (7.5–8.5); length of caudal peduncle (including both sexes) 5.7 (5.3–6.2); snout tip to origin of dorsal fin 1.8 (1.8–1.9); snout tip to origin of anal 1.3 (1.2–1.3).

Head and snout obtuse in vertical and horizontal profiles, top of head convex between eyes. Head 3.4 (3.2–3.6); eye in head 2.8 (2.7–2.9); snout in eye 1.3 (1.3–1.4); least width of bony interorbital in greatest eye diameter 1.0 (1.0–1.1).

Premaxillary with 6 to 7 teeth, each quinque- to tricuspid, sometimes most anterior tooth with only 4 cusps; lateral cusps largest. In large specimens, largest cusp just medial to lateralmost cusp; cusps subequal in some specimens. Only 1 specimen, SU 50219 from Brazil, with any maxillary teeth; this specimen with 1 conical tooth on 1 side only. Dentary with 7 to 8 quinque- or sexcuspid teeth in first outer row. Most posterior tooth in dentary conical, bicuspid, or tricuspid. Specimens from Brazil (except specimens from Obidos) having dentary with quinquecuspid teeth, central cusp being largest. Specimens from British Guiana with lower jaw teeth having either 6 subequal cusps or 5 cusps with a large central cusp. Smallest Brazilian specimen with lower jaw teeth having almost subequal cusps, while some of largest specimens from British Guiana with very large central cusps on quinquecuspid teeth. Specimens from Obidos with 6 subequal cusps on lower jaw teeth and 5 subequal cusps on upper jaw teeth. Teeth 6 to 7 in second tooth row of dentary. Gill rakers 7+12 in all alizarin preparations.

Dorsal fin rays ii,8; anal iii,9; pectoral i,10 to i,13; pelvics ii,7. Adipose fin absent in all specimens examined. Caudal fin with principal rays 10/9; distal tips of all ray elements of first 10 principal rays in upper caudal lobe. Lower caudal lobe containing all elements of remaining 9 principal rays.

Anal fin of male and female alike. Rays of male's anal fin not modified. Inclinator muscle appears slightly, if at all, more developed in male than in female.

Radial grooves of scales in third horizontal scale series lying below dorsal fin shown in figure 8. Posterior field with 1 to 3 radial grooves. Dorsal and ventral fields each with 1 radial groove and anterior field with 2 to 4 radial grooves. Scales 21 to 23 in lateral series in all specimens examined and 3 to 5 lateral-line scales (usually 4); 10 scales in median predorsal series. Total number of vertebrae 31 to 33. Of 35 specimens from localities in Brazil, 32 with 32 vertebrae, 2 with 31 vertebrae and 1 with 33 vertebrae. Of 15 specimens from localities in British Guiana 9 specimens with 31 vertebrae, 1 with 33 vertebrae

and 5 with 32 vertebrae. Precaudal vertebrae 17 to 19 and caudal vertebrae 13 to 14, never in a combination over 33 or under 31 total vertebrae.

Color in alcohol.—(Specimens from British Guiana). Dorsum of head light to dark brown. Primarily horizontal stripe beginning on lower part of snout tip and tip of lower jaw, extending to pupil of eye, then passing over posterior part of iris, across fourth and fifth orbitals to posterior edge of operculum. Primary horizontal stripe then continuing from under fleshy opercular flap posteriorly over lower portion of third scale row and upper half of fourth scale row to terminate as narrow black wedge on caudal fin. On caudal peduncle, primary horizontal stripe expanding downward to cover all but lowermost ventral scale row.

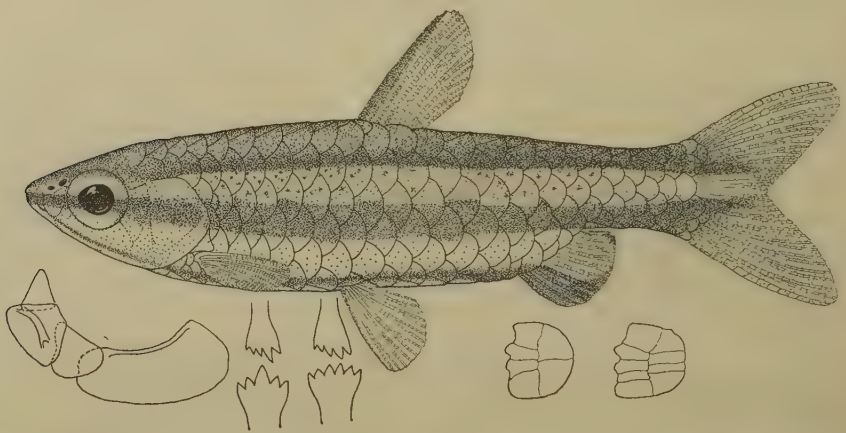

Figure 8.—*Nannostomus marginatus*, male, SL 19.5 mm., CAS(IUM) 11700 (see text for discussion of teeth).

Pale silvery stripe extending from eye onto caudal fin above primary horizontal stripe. Melanophores scattered over entire surface of this silvery stripe, thickest and heaviest in region of third through about eighth and thirteenth or fourteenth to sixteenth vertical scale rows. These darker areas representing oblique bands, one anterior, one posterior to dorsal fin. Silvery band most pale over hypural fan and on caudal fin between wedge-shaped portions of primary and secondary horizontal stripes. Secondary horizontal stripe dorsal to pale lateral stripe. Secondary stripe extending above opercular bone through upper part of second lateral scale row onto caudal fin, terminating on this fin as an acute wedge. Dorsum dark above secondary horizontal stripe, rather densely covered with melanophores, especially behind dorsal fin. Below primary horizontal stripe, sides white to very pale

brown with few scattered melanophores. Tertiary horizontal stripe extending along sides of belly through sixth lateral scale row and across head over preopercle and third orbital bone to angle of jaw. Sometimes this stripe reduced in region of pectoral fins. Pectoral fin translucent; pelvic fin same except for thin line of melanophores along anterior 2 rays in some specimens. Dorsal fin dusky at its anterior base, its first two unbranched rays dark. Almost entire lower half of anal fin dark brown to black; its distal edge and upper edges also dark.

Color in life.—The color of aquarium specimens which are from an unknown locality, but which agree with Eigenmann's (1909, p. 42) brief color description of his material from British Guiana, is as follows: Midanterior region of dorsal fin with one red spot, ventral region of anal fin red; medial half of pelvic fins red. Color photo in Axelrod and Schultz (1955, p. 241) shows position of this red pigment well. A short red stripe along midupper border of primary horizontal stripe (which is black in life); half of this stripe on primary horizontal stripe and half on pale golden stripe above black horizontal stripe. This red stripe extending from about sixth to ninth vertical scale rows. A few streaks of white pigment at posterior end of pale gold band above primary horizontal stripe. This white pigment mostly confined to caudal fin rays between wedges of primary and secondary horizontal stripes. Lateral surface of the snout pale gold. Iris pale gold where melanin absent. Belly and region below primary horizontal stripe silvery white. Distal anterior parts of pelvics white.

Aquarium specimens which agree well with specimens recorded below from the lower Amazon have the following color: Red of fins almost absent except on dorsal fin. Red stripe on side of body absent. Secondary and tertiary horizontal stripes somewhat broader and more sharply delineated. Stripe above primary horizontal stripe not as golden as in presumed British Guiana specimens. Belly and area below primary horizontal stripe brownish white. White spot on caudal fin between wedges of primary and secondary horizontal stripes more intense.

Living specimens collected by White, Reynolds, and Wulff (see list of specimens below) from Colombia near Tres Esquinas have the following color: Proximal two-thirds and often entire length of fourth to sixth dorsal fin rays bright orange red. First 3 dorsal rays black, seventh to tenth rays and adjoining tissue hyaline. Middle rays of caudal fin red between dark caudal wedges (this region occupied by intense white in living specimens presumably from lower Amazon). Pelvic fins red except for anterior black border. Anal fin from its middle and posterior base out to one-third or three-quarters of its distal surface varying from silvery to golden yellow. Anterior base

of pelvic fin and distal portion of its anterior 4 to 5 rays bright red. Distal tips of second to about fourth pelvic rays black. Belly silvery; area below primary horizontal stripe bright gold. Entire length above primary horizontal stripe with narrow iridescent gold or sometimes silvery-red stripe. Above this with a greenish dark-brown area, same color as top of head and dorsum. Primary, secondary, and horizontal stripes black. Iridescent golden to pale reddish spot near anterior nostril.

Remarks.—*Nannostomus marginatus* has been reported only from the Guianas. It now appears to be a widespread polymorphic species found in the Guianas and in at least several widely separated areas in the Amazon Basin. Hoedeman's subspecies *picturatus* from Surinam is described very inadequately and some of the description appears to be in error. For example he reported a difference in caudal fin ray counts between the British Guiana and Surinam populations. He stated the caudal rays to be 10+10 in specimens from British Guiana and 8 to 9+9 to 8 in specimens from Surinam. All specimens of nannostominans and indeed all characids that I have examined, except for a few obviously abnormal specimens of the genera *Hyphessobrycon* and *Moenkausia*, have had a principal caudal fin ray count of 10/9 (equals 10+9). I am not sure whether Hoedeman counted principal caudal fin rays or only unbranched rays. However, he reported the wrong count for either method. It should be noted that in counting the principal caudal rays of two of Hoedeman's types of *N. bifasciatus*, the typical count of 10/9 was found. Hoedeman (1954a) reported 8(7)+8(7). Despite the probable errors in some of Hoedeman's counts, and possibly also his measurements, probably it will be found eventually that his subspecies *picturatus* is valid. Also the populations noted here from lower and upper Amazon Basin very probably will, when adequate material becomes available, prove to be sufficiently different to merit subspecific recognition. An example of the difference in teeth of different populations can be seen in figure 8. The two opposing teeth to the right are from British Guiana specimens [CAS (IUM) 11700] while those to the left are from Lagôa Grande, Brazil (SU 50219).

Specimens examined.—Four, paratypes, CNHM 52776, SL 17.0–18.5 mm., Brutish Guiana, Maduni Creek, Mahaica River, 1908, Carl H. Eigenmann.—Two, CNHM 54932, SL 19.4–20.3 mm., British Guiana, Hubabu Creek, Demerara River, Oct. 1, 1910, Max Ellis.—One, paratype, SU 21941, SL 17.6 mm., British Guiana, Cane Grove Corner, Mahaica River, 1908, Carl H. Eigenmann.—Two, paratypes, CAS(IUM) 11697, SL 16.0–16.4 mm., British Guiana, Lama Stop-Off, Mahaica River, 1908, Carl H. Eigenmann.—One, paratype, CAS(IUM) 11698, SL (damaged), British Guiana, Crab Falls, Essequibo River, 1908, Carl H. Eigenmann.—One, paratype, CAS(IUM) 11699, SL 19.5 mm., British Guiana, Rockstone sandbank, Essequibo River, 1908, Carl H. Eigenmann.—Two, para-

types, CAS(IUM) 11700, SL 19.5–21.8 mm., British Guiana, Gluck Island, Essequibo River, 1908, Eigenmann.—One, paratype, CAS(IUM) 11701, SL (damaged), British Guiana, Christianburg Canal, Demerara River, 1908, Eigenmann.—Five, paratypes, CAS(IUM) 11702 (one alizarin preparation), SL 17.5–18.0 mm., British Guiana, Cane Grove Corner, Mahaica River, 1908, Eigenmann.—Thirty-two, SU 50219 (three alizarin preparations), SL 15.0–22.8 mm., Brazil, State of Pará, Lagôa Grande, Igrapé do Meritysál (probably Lagôa Grande do Javafy about 34 miles northwest of Santarém), Aug. 20, 1924, Carl Ternetz.—Four, SU 50218, SL 16.4–19.5 mm., Brazil, State of Pará, Igrapé Uruará, tributary of the Furo Maica about 10 miles southeast of Santarém, June 26, 1924, Carl Ternetz.—Two, MCZ 19645, SL 23.5–25.4 mm., Brazil, State of Pará, Obidos, 1865, Col. Bentos, Thayer Expedition.—Two, SU 50217, SL 20.0–22.0 mm., Brazil, State of Pará, Lagôa Grande (probably Lagôa Grande do Javafy about 34 miles northwest of Santarém), a stream into Ajamurí beach, July 17, 1924, Carl Ternetz.—One, SU 50555, SL 18.0 mm., Colombia, Caquetá Province, swampy pond about one-fourth mile inland from Río Orteguaza, across the river and slightly below Tres Esquinas, lat. 0°54′ N. and long. 75°15′ W., Feb. 8, 1958, 8–10 a.m., Gen. T. D. White, Col. J. N. Reynolds, Lee Wulff, and Dr. George S. Myers.—One, SU 50669, SL 16.5 mm., Colombia, Caquetá Province, small stream across Rio Orteguaza from Tres Esquinas, lat. 0°45′ N., long. 75°15′ W., Feb. 13, 1958, Gen. T. D. White, Col. J. N. Reynolds, Lee Wulff and Dr. George S. Myers.—Twenty-six, SU 50628, SL 16.0–22.1 mm., Colombia, Caquetá Province, small forest tributaries of Río Orteguaza on road from Tres Esquinas to Solano, lat. 0°45′ N., long. 75°15′ W., Feb. 12, 1958, Gen. T. D. White, Col. J. N. Reynolds and Lee Wulff.—Six, SU 50457, SL 18.0–18.4 mm., British Guiana, Ishalton, southern Rupununi District, Rupununi River drainage, tributary of Essequibo River, Dec. 12, 1957, Rosemary Lowe (McConnell).—Two, SU 50445, SL 17.5–19.6 mm., British Guiana, Atkinson Field Creek, near Hyde Park, tributary of Demerara River, Nov. 11, 1957, Rosemary Lowe (McConnell).—Eight, SU 50451, SL 16.0–17.0 mm., British Guiana, Kumarow Creek pool, tributary of Rupununi River in southern savannas, Essequibo River drainage, Dec. 10, 1957, Rosemary Lowe (McConnell).—Twenty-six, SU 50452, SL 16.2–18.7 mm., British Guiana, creek approximately 5 mi. south of Lumidpau, southern Rupununi savannas (flows into Rupununi River), Essequibo drainage, Dec. 11, 1957, Rosemary Lowe (McConnell).—Twenty-five, SU 50441, SL 15.7–19.5 mm., British Guiana, Rupununi District, Nappi River and other Tacatú drainage creeks, Rio Branco drainage, Sept. 20, 1957, Rosemary Lowe (McConnell).—Five, SU 50428, SL 16.5–19.0 mm., British Guiana, Manawarin River, tributary of the Moruka River about lat. 7°30′ N. and long. 59°00′ W., July 16, 1957, Rosemary Lowe (McConnell).

Genus *Poecilobrycon* Eigenmann

Poecilobrycon Eigenmann, 1909, p. 43 (type species *Poecilobrycon harrisoni* Eigenmann, 1909, by original designation).

Archicheir Eigenmann, 1909, p. 46 (type species *Archicheir minutus* Eigenmann, 1909, by monotypy).

Nannobrycon Hoedeman, 1950, p. 22 (type species *Nannostomus eques* Steindachner, 1876, by original designation).

Diagnosis.—The following two characters appear unique for this genus: Second infraorbital bone with a bony canal for infraorbital branch of latersensory canal. In addition, snout long, 0.8 to 1.2

in eye diameter. The members of this genus have, correlated with the long snout, a longer, narrower ethmoid and prevomer, a longer antorbital and infraorbital, and a longer mesopterygoid and nasal bone than do members of the genus *Nannostomus*. Primary and secondary horizontal stripes are present in all species, but a tertiary horizontal stripe is absent in 2 species. The anal fin rays may or may not be modified in males. The body is elongate in all species, the depth being 4.5 to 5.7 in standard length.

The name *Poecilobrycon* is derived from the generic names *Poecilia* and *Brycon*, the implied meaning being a *Poecilia*-like *Brycon*, i.e., a *Brycon*-like fish or characid with characters of the poeciliid fishes. This name probably occurred to Eigenmann because of the small mouth and numerous tooth cusps in *Poecilobrycon*. However, in detail, the mouth of nannostominans bears little resemblance to that of any poeciliid fish.

Subgenus *Poecilobrycon* Eigenmann

DIAGNOSIS.—As in all members of *Nannostomus*, 10 principal rays of upper 4 hypural bones all enter upper caudal lobe. Lower lobe of caudal fin with dark pigment only at its base. Normal resting and swimming position horizontal. See under the subgenus *Nannobrycon* for a discussion of this character.

Poecilobrycon harrisoni Eigenmann

FIGURES 9, 10

Poecilobrycon harrisoni Eigenmann, 1909, p. 43 (original description; type locality: British Guiana, Canal at Christianburg, Demerara River; holotype in Chicago Natural History Museum); 1910, p. 427 (listed); 1912, p. 284, pl. 37, fig. 1 (description; British Guiana).—Hoedeman, 1950, p. 22 (copied description); 1954b, p. 89 (description; British Guiana).—Weitzman, 1964, p. 136 (osteology and relationships).

Archicheir minutus Eigenmann, 1909, p. 46 (original description; type locality: British Guiana, Canal at Christianburg, Demerara River; holotype in Chicago Natural History Museum); 1910, p. 427 (listed); 1912, p. 287, pl. 37, fig. 5 (description; British Guiana).

?*Nannostomus kumuni* Ladiges, 1948, p. 30 (name only listed, nomen nudum).

?*Nannostomus cumuni* Arnold, 1950, p. 63 (original description, from life, no type specimens).

DIAGNOSIS.—This species may be distinguished from all other nannostominans by its greater number of vertebrae, 38 to 39, contrasted to 31 to 36. It may be recognized further by the following combination of characters: Second tooth row of dentary with 12 to 15 teeth; 7+13 gill rakers; iii,9 anal fin rays; 27 to 30 scales in lateral series; maxillary tooth present; fairly long caudal peduncle, 5.3–6.1 in standard length.

DESCRIPTION.—Body elongate, slender, sides only slightly flattened anteriorly and caudal peduncle compressed. Greatest depth lying just anterior to anterior base of dorsal and anal fins. Standard length of largest specimen 44.5 mm. One old aquarium specimen reached a standard length of 44.0 mm. after living 2½ years. Greatest body depth 5.4 (4.9–5.7); least depth of caudal peduncle 10.9 (10.4–12.1); length of caudal peduncle (including both sexes) 5.7 (5.3–6.1); snout tip to origin of dorsal fin about 1.9 in all adult specimens; snout tip to origin of anal fin about 1.3 in all adult specimens.

Head elongate and somewhat depressed. Top of head very slightly convex between eyes. Snout rounded in horizontal and vertical profiles. Head 4.0 (3.8–4.1); eye in head 3.2 (3.0–3.2); snout in eye 0.9 (0.8–1.0); least width of bony interorbital in greatest eye diameter 1.1 (1.0–1.2).

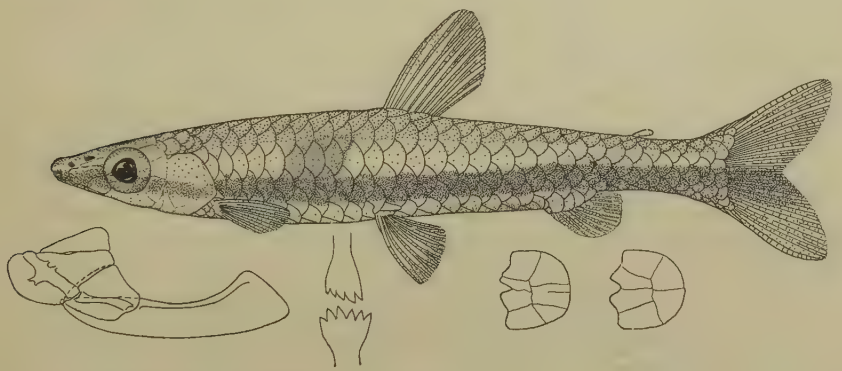

FIGURE 9.—*Poecilobrycon harrisoni* male, SL 38.5 mm., SU 50243.

Premaxillary with 7 quadri- to septemcuspid teeth. Most with 5 or 6 cusps; cusps subequal or posterolateral cusps most prominent. Maxillary with 1 conical, bicuspid, or tricuspid tooth. Dentary with 7 to 8 (usually 8) teeth in first row. Posterior 2 teeth with 3 to 5 subequal cusps, remainder of teeth in first row with 6 subequal cusps. Second dentary tooth row of about 12 to 15 small conical teeth. Gill rakers 7+13 in alizarin preparations.

Dorsal fin rays ii,8; anal iii,9; pectoral i,10 to i,11; pelvic fin rays ii,7. Adipose fin varying from well developed to rudimentary or absent. Caudal fin with principal rays 10/9; distal tips of all ray elements of first 10 principal rays included in upper lobe. Lower caudal lobe with all elements of remaining 9 principal rays.

Radial grooves of scales in median series below dorsal fin shown in figure 9. Posterior field with 1 to 4, dorsal and ventral fields 1, and anterior field 2 to 5 or 6 radial grooves. Scales in a lateral series 27

to 30 (usually 29). Lateral-line scales 3 to 5, usually 4. Scales in a median series in front of dorsal fin 11 to 13, usually 12. Total number of vertebrae 38 to 39 with 21 precaudal and 17 to 18 caudal vertebrae.

Color in alcohol.—Specimens from British Guiana, SU 50446, have the following colors: (The paratypes are coated rather heavily, apparently with lead oxide from a metal number tag, but agree well with the description below.) Top of head light to dark brown. Primary horizontal stripe extending from snout tip and lower jaw posteriorly over maxillary, first and second orbitals, and onto eye. From posterior part of eye, primary horizontal stripe extending to posterior edge of opercular bone. On body, primary horizontal stripe continuing from under fleshy opercular flap posteriorly through fourth scale row and part of fifth to caudal peduncle and caudal fin; on caudal peduncle extending over ventral body surface. On caudal fin, primary horizontal stripe not taking form of a narrow wedge but expanding to cover upper part of lower caudal lobe.

Above primary horizontal stripe a pale stripe extending from snout tip to caudal base. Dark area on sixth through eight vertical scale rows. Aggregation of melanophores on pale stripe vertically above anal fin. Secondary horizontal stripe apparently absent; entire dorsum above middle of second horizontal scale row light brown. Belly silvery, but posterior to pelvic fins in males becoming dusky. Pectoral fins translucent. Dorsal fin slightly dusky anterodistally but otherwise translucent and pelvics clear except for dusky distal band. Upper lobe of caudal fin slightly dusky. Anal fin translucent; in some specimens last ray black.

Color in life.—The colors of aquarium specimens, SU 50246, from Demerara River, British Guiana, are as follows: Dorsal and pectoral fins hyaline. Pelvic fin of male with proximal one-third to three-fourths of fourth to ninth pelvic rays orange red. These fins hyaline in female. Distal one-third of third through fourth pelvic rays and adjacent membrane silvery blue in both sexes. Anal fin of female hyaline with occasionally one spot of silvery blue on distal one-fourth of fourth anal fin ray. Male also with silvery blue disposed in same manner but proximal one-third to one-half of all anal fin rays bright red. Proximal portions of caudal fin lobes red above and below extension of primary horizontal stripe on fin rays. These areas silvery yellow with faint indications of red in females. Primary horizontal stripe black. Above this stripe a narrow silvery band and above this body shades to light or sometimes brown on dorsum. Metallic-red spot near anterior narial opening. Belly and sides below primary horizontal stripe white.

Remarks.—So far as is known *Poecilobrycon harrisoni* is restricted

to British Guiana. All the aquarium specimens that I have seen over the past 10 years have had approximately the same color pattern. Thus it appears that aquarium fish collectors are collecting all their specimens from the same general area. Very probably this is from the vicinity of Georgetown in tributaries of the Demerara River, British Guiana, where the fishes are known to occur and where collectors are known to have been active in the last several years. In many respects, the color and breeding habits of *Poecilobrycon harrisoni* are like those of *Nannostomus beckfordi* suggesting that the two may have been derived from a common ancestor and may be related more closely than their morphology indicates.

The type of *Archicheir minutus* is the young of *Poecilobrycon harrisoni*. The type was studied at the Chicago Natural History Museum and found identical with young specimens of *harrisoni* spawned and raised in the author's aquarium.

SPECIMENS EXAMINED.—Two, paratypes, CAS(IUM) 11709, SL 36.5–41.5 mm., British Guiana, Canal at Christianburg, Demerara River, 1908, C. H. Eigenmann.—Four, SU 50243, SL 34.0–38.0 mm., British Guiana, Georgetown.—Twelve, SU 50245 (one alizarin preparation), SL 31.0–37.5 mm., British Guiana, no other data.—Three, SU 50244, SL 13.3–44.5 mm., aquarium specimens, Aug. 21, 1956, S. H. Weitzman.—Eight, SU 50246, SL 9.5–37.5 mm., aquarium specimens from Demerara River, British Guiana, and their young aquarium spawned and raised, S. H. Weitzman.—Seven, SU 50446, SL 17.0–44.5 mm., British Guiana, Atkinson Field Creek, near Hyde Park, tributary of the Demerara River, Nov. 11, 1957, Rosemary Lowe (McConnell).

Subgenus *Nannobrycon* Hoedeman

DIAGNOSIS.—Rays of caudal fin arranged unlike those of all other nannostominans; 10 rays of upper 4 hypural plates not all entering upper caudal lobe. Lowermost 2 of these rays enter lower caudal lobe, giving that lobe greater depth than upper lobe. Lower caudal lobe usually with dark pigment extending well onto fin, sometimes over its entire surface. Normal resting position of living members of this subgenus oblique, snout upwards. Angle of this oblique position is from about 45° to about 75° or 80°.

REMARKS.—Hoedeman (1950) proposed *Nannobrycon* as a generic name for *Poecilobrycon eques* (Steindachner). In it he included only this species, believing *P. unifasciatus* to be a synonym of *P. eques*. Both species of this subgenus have the same peculiar caudal fin structure and behavior mentioned above. Hoedeman (1950) noted that the shape of the swim bladder of the members of this subgenus is different from those of all other nannostominans that he examined. However, he did not examine the swim bladder of *Poecilobrycon harrisoni*, as he had no specimens. The swim bladder differences that Hoedeman noted were crudely presented and are not suitable to distinguish *harrisoni* from *eques* and *unifasciatus*. However, the

normal resting position of members of the subgenus *Nannobrycon* is so different from that of the single known member of the subgenus *Poecilobrycon*, and indeed from all other known nannostominans, that there is undoubtedly a difference in shape correlated with this swimming position. Critical morphological examination of the organs of equilibrium, the swim bladder, and musculature of the caudal fin of all nannostominans will possibly show sufficient differences for *Nannobrycon* to be retained as a full genus. Braemer and Braemer (1958) have started a project studying the behavior and position of the utricular statolith with reference to *Poecilobrycon eques* and other characids.

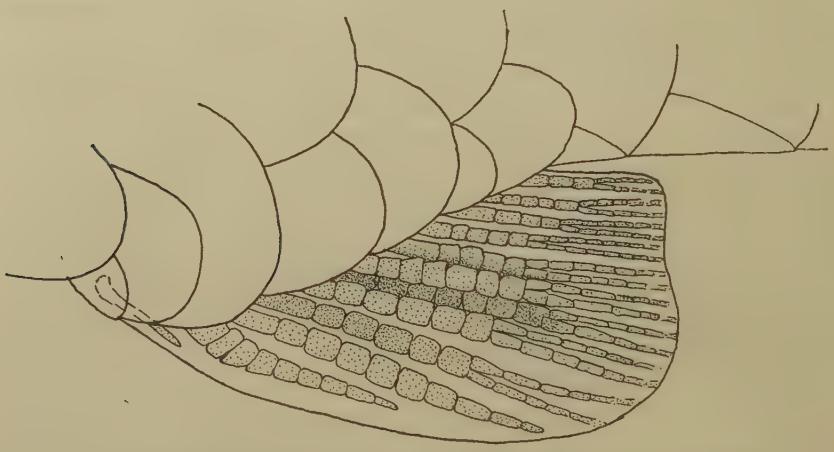

FIGURE 10.—Anal fin of *Poecilobrycon harrisoni*, SL 38.5 mm., SU 50243.

Poecilobrycon unifasciatus (Steindachner)

FIGURE 11

Nannostomus unifasciatus Steindachner, 1876, p. 127, pl. 9 (original description; localities: Mouth of the Rio Negro and Teffé on the Solimoens; types in Vienna Museum).—Eigenmann and Eigenmann, 1891, p. 49 (listed); 1910, p. 427 (listed).—Sterba and Tucker, 1962, p. 214 (description and aquarium notes; photographs are of *P. harrisoni;* also part of color description seems to refer to this species).

Poecilobrycon ocellatus Eigenmann, 1909, p. 45 (original description; type locality: British Guiana, Wismar, Demerara River, holotype in Chicago Natural History Museum); 1910, p. 427 (listed); 1912, p. 286, pl. 37, fig. 4 (description).

Poecilobrycon unifasciatus—Innes, 1935, p. 158 (description from life and photograph).—Axelrod and Schultz, 1955, p. 249 (description and aquarium notes).

Poecilobrycon eques (in part).—Hoedeman, 1950, p. 23.

Nannostomus ocellatus—Sterba and Tucker, 1962, p. 214 (description and aquarium notes).

DIAGNOSIS.—This species may be distinguished from all other nannostominans examined by the complete absence of a second row

of teeth in the dentary; in addition, it may be distinguished by the following combination of characters: Adipose fin present; 33 to 34 vertebrae; 2 to 5 perforated scales in the lateral line; iii,9 anal fin rays; 9+14 gill rakers and 28 to 30 scales in a lateral series.

Description.—Body elongate, slender, and somewhat cylindrical anteriorly, but sides somewhat flattened; compressed posteriorly. Greatest depth anterior to dorsal fin and posterior to distal tips of appressed pectoral fins. Standard length of largest specimen 38.3 mm. Greatest body depth 5.0 (4.7–5.3); least depth of caudal peduncle 10.4 (10.0–11.2); length of caudal peduncle (including both sexes) in specimens listed below from Brazil 6.9 (6.7–7.5) and from British Guiana 6.2 (6.0–6.6); snout tip to origin of dorsal fin 1.9 (1.8–1.9); snout tip to origin of anal fin 1.2 (1.2–1.3).

Head elongate, somewhat depressed, especially over snout. Top of head slightly convex between eyes. Snout rounded in horizontal profile. Head 3.9 (3.9–4.0); eye in head, Brazilian specimens 3.0 (2.8–3.2), British Guiana specimens 3.4 (3.2–3.4); snout in eye 1.0 (0.9–1.2); least width of bony interorbital in greatest eye diameter 1.1 in all specimens from Brazil and 1.0 in all specimens from British Guiana.

Premaxillary with 6 to 7 quinquecuspid teeth. Posteriomost lateral tooth sometimes with only 3 to 4 cusps. Each maxillary with 1 quadricuspid tooth. Dentary with 6 or 7 quinque- or sexcuspid teeth, cusps subequal. Second row of dentary absent in all alizarin specimens. Gill rakers 9+14.

Dorsal fin rays ii,8; anal iii,9; pectoral i,9 to i,11; pelvics ii,7. Adipose fin present in all specimens examined. Caudal fin with principal rays 10/9. Distal tips of 8 principal rays in upper lobe and 11 in lower lobe.

Anal fin of males slightly modified. Male specimens examined from Venezuela and Brazil with anal fin shape as shown in insert in figure 11. This shape approaches that of anal fin of *Poecilobrycon eques* but fin of *P. unifasciatus* not as large. Second undivided ray expanded anteriorly and posteriorly, giving this ray a flattened appearance. Posterior margin of this ray fits into recess formed by 2 ray halves of expanded and flattened third unbranched ray behind. First branched ray with slight recess for the enlarged third ray. Inclinator muscle only slightly developed and beyond basal scales attached to ninth ray only. Specimens from British Guiana with anal fin of male less developed than specimens from Brazil and Venezuela. Anal fin of specimen from British Guiana resembles that of entire specimen in figure 11. Second and third unbranched and first and second branched rays only slightly enlarged. Anal fin of female from British Guiana, Brazil, and Venezuela with rays not at all enlarged. Male specimens from Brazil

and Venezuela shorter than about 24 mm. in standard length with anal fins much like those of males from British Guiana. Possibly anal fin develops its pointed posterior border only in males longer than about 29 mm. in standard length.

Radial grooves of scales in that part of third horizontal scale series below dorsal fin rather variable but frequently resemble scales in figure 11. Posterior field with 1 to 3 (most frequently 2) radial grooves, dorsal and ventral fields with 1 and anterior embedded field with 2 to 6 radial grooves. Scales in a lateral series 28 to 30 (usually 29) and 2 to 5 (usually 4) scales in lateral line. Scales in a median series before the dorsal fin 11. Total number of vertebrae 33 to 34 with 21 precaudal and 12 to 13 caudal vertebrae. British Guiana

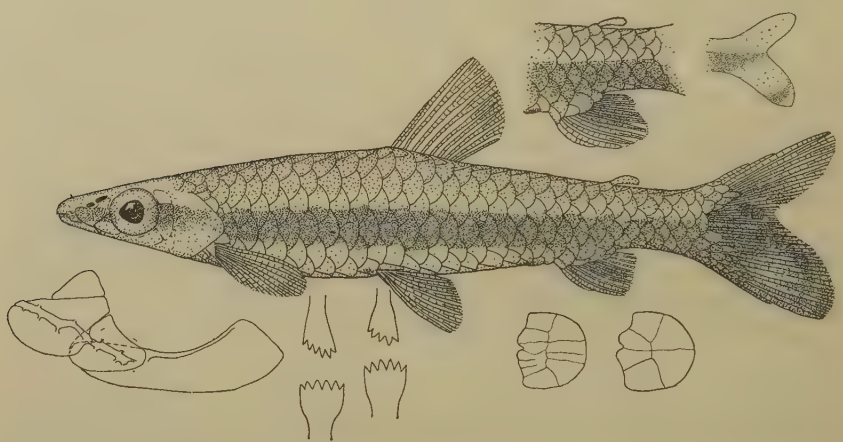

FIGURE 11.—*Poecilobrycon unifasciatus*, male, SL 33.4 mm., CAS(IUM) 11703 (see discussion for remarks on insert drawings of anal and caudal fins).

specimens all with 34 vertebrae and all specimens recorded below from Igarapé do Mãi Joana, near Manáos, with 33 vertebrae. Of specimens examined from Teffé, both with 33 vertebrae.

COLOR IN ALCOHOL.—(Specimens from British Guiana) Dorsum of head light brown. Primary horizontal stripe beginning on snout and lower jaw, extending posteriorly over maxillary and first orbital bone onto eye. Posteriorly from iris this stripe continuing across part of fourth and fifth orbitals to across opercular bone, not present on fleshy opercular flap and extending through fourth scale row to end of caudal peduncle as shown in figure 11. On caudal peduncle primary horizontal stripe expanding ventrally to include entire ventral area. On caudal fin primary horizontal stripe covering entire lower lobe except for crescent near lower posterior margin and central clear area

as shown in figure 11. Upper lobe dusky near its basal, lower portion, and this dusky region with dark spot (ocellus) with a translucent area around it. Secondary horizontal stripe appearing absent and entire back light brown. Belly bright silvery with a dark spot in front of vent and a very small dark spot in front of pelvic fin base. Head below primary horizontal stripe bright silver. Pectoral, dorsal, and anal fins translucent. Anal fin with single dark spot in its basal and central regions. Preserved specimens from Brazil and Venezuela not differing in color except in caudal fin. Specimens from these areas lack an ocellus, except one from Venezuela with an imperfect ocellus. Also markings on lower lobe of caudal fin somewhat different. These well shown in figure accompanying Steindachner's original description. Preserved specimens from Igarapé do Mãi Joana at Manáos, with primary horizontal stripe extending onto caudal fin as a narrow wedge, and distal region of caudal fin dusky to dark (see upper right insert in fig. 11). Steindachner's figure shows primary horizontal stripe extending onto caudal fin as slightly widening band. However, all specimens that I have examined from Brazil and Venezuela with a caudal fin color pattern about as that shown in the upper right insert in figure 11.

Color in life.—Aquarium specimens from an unknown locality (but agreeing well with color of preserved specimens from British Guiana) had the following color pattern: Dorsal and pectoral fins hyaline; pelvic fin also hyaline except for second and longest ray, which is silvery blue on distal one-third to one-half of its length. Anal fin hyaline except for central black blotch and silvery white distal tips of fourth to seventh rays. Caudal fin variously colored, the upper lobe hyaline; area dorsal to black ocellus white, and below it creamy yellow to rich orange. Nonmelanistic areas on the lower caudal fin lobe creamy white to yellow suffused with varying shades of orange. Belly and throat regions white. Area below primary horizontal stripe white. Silvery white stripe especially distinct behind dorsal fin above black primary horizontal stripe. Above silvery stripe, dorsum and top of head light to medium brown. Bright metallic-orange spot near the anterior narial opening.

Remarks.—*Poecilobrycon unifasciatus* was known previously only from the mouth of the Rio Negro and Teffé and (under the name *Poecilobrycon ocellatus*) from British Guiana. The records listed below considerably enlarge its known range up the Rio Negro to the headwaters of the Río Orinoco in Venezuela. Hoedeman (1950) apparently did not have specimens of the true *unifasciatus*, or if he did, he confused them with *P. eques*. Hoedeman stated that some of the young from parents with the typical color pattern of *eques* look

like typical *unifasciatus*. *Poecilobrycon eques* have spawned in my aquaria and I have raised the resulting young. Also I have seen young of *eques* raised by other aquarists. In none of these have I seen any specimens that look like *unifasciatus*. The description of *eques* given by Hoedeman is hard to follow and seems somewhat confused and inconsistent. However, his main thesis seems to be that the differences noted by Steindachner between *eques* and *unifasciatus* are those of age and sex. In any event, the descriptions given here should serve to distinguish *eques* and *unifasciatus* and put an end to further confusion. From the key and descriptions, it can be seen that the species are quite distinct in their morphology.

Specimens examined.—Thirteen, SU 50263 (three alizarin preparations, SU 50264), SL 27.0–34.8 mm., Brazil, State of Amazonas, Igarapé do Mãi Joana into Rio Negro near Manáos, Dec. 24, 1924, Carl Ternetz.—One, MCZ 19769, SL 31.5 mm., Brazil, State of Amazonas, Lake Hyanuary, near Manáos, 1865–1866, Thayer Expedition, Mr. Navez.—One, MCZ 19935, SL 28.0 mm., Brazil, Jutahý, 1865–1866, Thayer Expedition, James, Thayer and Tailisman.—Two, MCZ 19787, SL 29.0–38.3 mm., Brazil, Lake José Assú, 1865–1866, Thayer Expedition, Louis Agassiz.—Fifteen, MCZ 19591, SL 25.0–33.0 mm., Brazil, State of Amazonas, Teffé, 1865–1866, Thayer Expedition, Louis Agassiz.—Two, SU 50266, SL 23.0–27.2 mm., Venezuela, Río Orinoco, Caño de Quiribana, opposite Pan de Azúcar, near Caicara, May 7, 1925, Carl Ternetz.—Five, SU 50265, SL 26.0–33.0 mm., Venezuela, Río Orinoco, creeks at high water into Laguna San Raphael, Caicara, Apr. 28, 1925, Carl Ternetz.—Two (paratypes of *P. ocellatus* Eigenmann), CAS(IUM) 11703, SL 31.2–32.8 mm., British Guiana, Demerara River, Wismar, 1908, Carl H. Eigenmann.—Ten (paratypes of *P. ocellatus* Eigenmann), CAS(IUM) 11704 (one specimen as alizarin preparation), SL 29.6–34.0 mm., British Guiana, Rockstone sandbank, Essequibo River, 1908, C. H. Eigenmann.—Two (paratypes of *P. ocellatus* Eigenmann), SU 21963, SL 31.8–33.5 mm., British Guiana, Rockstone, Essequibo River, 1908, Carl H. Eigenmann.—Three (paratypes of *P. ocellatus* Eigenmann), CAS(IUM) 11705, SL 29.2–37.1 mm. and three (paratypes of *P. ocellatus* Eigenmann) CNHM 52782, SL 32.0–34.0 mm., British Guiana, Gluck Island, Essequibo River, 1908, Carl H. Eigenmann.—Three (paratypes of *P. ocellatus* Eigenmann), CAS(IUM) 11706, SL 28.2–29.2 mm., British Guiana, Rupununi, Essequibo drainage, 1908, C. H. Eigenmann.—One (paratype of *P. ocellatus* Eigenmann), CAS(IUM) 11708, SL 30.0–33.5 mm., British Guiana, Konawaruk, Potaro River, 1908, C. H. Eigenmann.—Two, SU 19049, SL 31.0–34.4 mm., British Guiana, no other data.—Three, SU 19048, SL 27.0–28.0 mm., British Guiana, no other data.—One, SU 25613, SL 29.5 mm., aquarium specimen, no other data.—Two, SU 50267, SL 30.1–30.5 mm., aquarium specimens, no other data.—Two, SU 50268, SL 27.8–30.4 mm., alizarin preparations, aquarium specimens, no other data.—One, SU 50438, SL 30.6 mm., British Guiana, Karanambo, "Grass Pond," Rupununi River, Essequibo drainage, Sept. 19, 1957, Rosemary Lowe (McConnell).—Three, SU 50435, SL 23.2–31.4 mm., British Guiana, Moreby Creek, Rupununi River near Karanambo, Essequibo drainage, Sept. 17, 1957, Rosemary Lowe (McConnell).

Poecilobrycon eques (Steindachner)

FIGURE 12

Nannostomus eques Steindachner, 1876, p. 126, pl. 9, fig. 3 (original description; type locality: Peruvian Amazon above Tabatinga; types in Vienna Museum).—Eigenmann and Eigenmann, 1891, p. 49 (listed).—Sterba and Tucker, 1962, p. 215 (description and aquarium notes).

Poecilobrycon auratus Eigenmann, 1909, p. 43 (original description; type locality: British Guiana, canal at Christianburg; holotype in Chicago Natural History Museum); 1910, p. 427 (listed).—Innes, 1935, p. 156 (description from life and photograph).

Poecilobrycon trifasciatus.—(not Steindachner) Eigenmann, 1912, p. 284, pl. 37, fig. 2 (description).

Poecilobrycon eques.—Eigenmann, 1910, p. 427 (listed).—Eigenmann and Allen, 1942, p. 288 (listed).

Nannobrycon eques.—(in part) Hoedeman, 1950, p. 23 (description; photograph); 1954b, p. 82 (description; photograph); 1954b, p. 82 (description; photograph).

DIAGNOSIS.—The unique feature of this species is its five lateral horizontal stripes. In addition it may be distinguished from all other nannostominans by the following combination of characters: No perforated lateral-line scales; 24 to 25 scales in lateral series; 33 to 34 vertebrae; iii,9 anal fin rays; 16+24 gill rakers; 12 teeth in the second tooth row of dentary.

DESCRIPTION.—Body elongate, somewhat cylindrical through anterior half, but sides flattened and compressed posteriorly. Greatest depth occurs between posterior tip of appressed pectorals and anterior base of dorsal fin. SL of largest specimen 35.0 mm. (largest aquarium specimen examined, a female, with SL of 37.0 mm.). Greatest body depth 4.5 (4.0–5.1); least depth of caudal peduncle 10.0 (10.0–11.0); length of caudal peduncle (including both sexes) 6.7 (6.0–7.1); snout tip to origin of dorsal fin 1.7 (1.7–1.8); snout tip to origin of anal fin about 1.3 in all specimens examined.

Head elongate, rather acute in vertical profile with tip of snout obtuse. Snout region somewhat depressed. Top of head very slightly convex between eyes. Head 3.5 (3.5–3.7); eye in head 3.3 (3.0–3.5); snout in eye 0.9 (0.8–1.0); least width of bony interorbital in greatest eye diameter 1.0 (0.9–1.0).

Premaxillary with 8 to 9 teeth, each quadri- to quinquecuspid, cusp next to posterolateral one largest. Maxillary with 1 quadri- or quinquescuspid tooth, cusps subequal. Dentary with 7 to 9 quinque- to sexcuspid teeth. Posterior 1 or 2 teeth usually with 3 cusps. Either central cusp or 2 posterolateral cusps largest (fig. 12). About 12 teeth in second dentary tooth row. Gill rakers 16+24.

Dorsal fin rays ii,8; anal iii,9; pectoral i,9 to i,11; pelvics ii,7. Adipose fin present or absent, seemingly not correlated with geo-

graphical origin. Caudal fin with principal rays 10/9; distal tips of 8 principal rays in upper lobe and 11 in lower lobe.

Anal fin of males enlarged and modified, but not as greatly as in *Nannostomus digrammus*. Second undivided ray expanded anteriorly and posteriorly, giving this ray a flattened appearance. Posterior margin of this ray fits into recess formed by 2 ray halves of expanded and flattened third unbranched ray behind. First, second, and third branched rays slightly flattened and expanded, first to greatest extent. These rays slightly ribbed. Rest of anal fin rays almost normal, being only slightly heavier than usual type of characid fin ray. Inclinator muscle attached to ninth ray only.

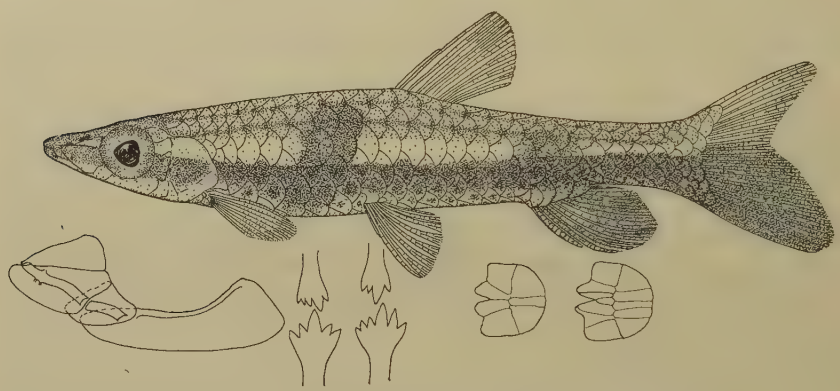

FIGURE 12.—*Poecilobrycon eques*, male, SL 29.0 mm., SU 50299.

Radial grooves of scales in third horizontal scale series below dorsal fin quite variable but general pattern shown in figure 12. Posterior field may have 1 to 4 radial grooves, anterior field 2 to 6 radial grooves and dorsal and ventral fields one radial groove each. Scales in a lateral series 24 to 25, no lateral-line scales and 11 or 12 predorsal scales. Total number of vertebrae 33 to 34, usually 18 to 19 precaudal and 15 caudal vertebrae.

COLOR IN ALCOHOL.—Top of head light brown. Nape, areas immediately above nares and eyes, central parts of frontals, and tip of snout, dark brown. Primary horizontal stripe beginning at tip of snout and lower jaw, extending posteriorly over first infraorbital to pupil of eye. Then extending from posterior edge of pupil to posterior edge of opercular bone. On opercle width of this stripe somewhat variable. On body, primary horizontal stripe beginning under fleshy opercular flap and extending posteriorly through entire fourth and fifth scale rows. In some specimens upper two-thirds of fourth scale row free of heavy pigment. Over anal fin

primary horizontal stripe extending dorsally to cover lower half of third scale row. On caudal peduncle primary horizontal stripe extending ventrally to cover entire lower half of caudal peduncle and then posteriorly to include entire lower lobe of caudal fin. On fifth row of scales primary horizontal stripe frequently confined to center of each scale, producing spotted appearance. In some specimens this shows well, in others pigment expanded and covering entire fifth row of scales, making primary horizontal stripe appear solid. Above primary horizontal stripe a broad pale-yellowish stripe covering lower two-thirds of horizontal scale row. This stripe beginning on snout above primary horizontal stripe and extending posteriorly through caudal peduncle to caudal fin. Weak scattering of melanophores over this band. Region of posterior part of sixth to posterior edge of eighth vertical scale rows with a dense aggregation of melanophores extending from middle of first to middle of sixth horizontal scale rows. These are oblique bands, and they appear faintly to strongly in all preserved specimens examined. A dense aggregation of melanophores occurs over anal fin. Entire dorsum light brown and secondary horizontal stripe consists of dense aggregation of melanophores through center of each scale in second horizontal scale row. Fourth narrow horizontal stripe extending through first horizontal scale row. Third horizontal stripe present as a series of dark spots along sixth horizontal scale row, each dot being in center of scale. Belly and upper parts of head clear yellowish white. In some specimens third horizontal stripe present on head as a thin dark stripe on third infraorbital bone. Adipose fin, when present, frequently black. Dorsal, pectoral, and pelvic fins hyaline. Anal fin almost entirely black except for clear area in its midbasal region. Second undivided ray also hyaline.

Color in life.—Aquarium specimens from an unknown locality had the following color pattern: Pectoral, dorsal, and upper lobe of caudal fins hyaline. Anal fin dark brown or black except for clear area mentioned above; this area bright orange red. Large second ray of anal fin silvery blue for about one-third its proximal length. Pelvic fins hyaline except for small amount of silvery blue pigment along large second fin ray. Lower lobe of caudal fin dark brown or black, variously and sparsely mottled with pale gold or orange. Some specimens with slight suggestion of an ocellus as in specimens of *unifasciatus* from British Guiana. Bright pale-gold blotch in region of caudal fin between two caudal lobes. Bright silvery stripe extending from snout tip to caudal peduncle above primary horizontal stripe. Dorsum light to medium brown except where covered by darker stripes described above. Pale orange or yellow metallic spot in region of nares. Belly and throat white.

REMARKS.—As noted above under *Poecilobrycon unifasciatus*, Hoedeman (1950) confused *unifasciatus* and *eques*. However, as the two descriptions presented here show, these two names are applied to quite distinct species. As noted on page 28, under the remarks about *Nannostomus trifasciatus*, Eigenmann (1909 and 1912) was apparently confused in regard to the identity of Steindachner's *trifasciatus* and *eques*. This probably led to the description of *auratus*, a synonym of *eques*. In any event, comparisons of specimens of *eques* (including those described as *auratus*) from British Guiana, widely separated parts of the Amazon and Rio Negro Basins, and from the headwaters of the Rio Orinoco, show that this species is remarkably constant in its color pattern throughout its range, more so than any other widely distributed nannostominan.

SPECIMENS EXAMINED.—One, SU 36898, SL 31.0 mm., Peru, Pévas [Pébas] District, Shansho Caño, Sept. 20, 1936, W. G. Scherer.—Two, SU 50236, SL 23.0–33.5 mm., Peru, Río Ampiyacu, near Pévas [Pébas], Aug. 16, 1940, W. G. Scherer.—Four, SU 50237, SL 21.8–27.0 mm., Peru, Pévas [Pébas], 1940, W. G. Scherer.—Two, SU 50226, SL 26.2 mm., Peru, Yaguasyacú, July 7, 1941, W. G. Scherer.—Five, SU 50229, plus two alizarin preparations SU 50247, SL 28.4–30.5 mm., Brazil, State of Amazonas, São Gabriel, Rio Negro, rock pools below rapids, Feb. 1, 1925, Carl Ternetz.—One, SU 50227, SL 29.2 mm., Venezuela, mouth of the Casiquiare, Feb. 24, 1925, Carl Ternetz.—Two, SU 50228, SL 31.5–32.9 mm., Venezuela, Caño de Quiribana, near Caicara, May 2, 1925, Carl Ternetz.—One, SU 50233, SL 31.4 mm., Brazil, State of Pará, Igarapé do Sapucúa into Lagôa Sapucúa (this lake drains into the Rio Trombetas, a tributary of the Amazon River), June 7, 1924, Carl Ternetz.—Three, SU 50230, SL 25.4–25.7 mm., Brazil, State of Pará, Cabeceira Maturaca into Lagôa Grande, Nov. 1924, Carl Ternetz.—Four, SU 50231, SL 24.3–25.0 mm., Brazil, State of Amazonas, Igarapé do Mãi Joana, into Rio Negro near Manáos, Dec. 25, 1924, Carl Ternetz.—Three, SU 50232, SL 26.5–26.6 mm., Brazil, "Pará, Juntil lago Jará," Apr. 4, 1924, Carl Ternetz.—Six, MCZ 6312, SL 23.5–27.5 mm., Brazil, State of Amazonas, Lake Hyanuary, near Manáos, Oct. 28, 1865, Thayer Expedition, Louis Agassiz.—Three, MCZ 19473, SL 21.5–24.4 mm., Brazil, State of Amazonas, Villa Bella, 1865–1866, Thayer Expedition, Louis Agassiz.—Two, MCZ 19594, SL 24.0–24.5 mm., Brazil, State of Amazonas, region of Tabatinga, Sept. 20 to Oct. 20, 1865, Thayer, Expedition, Bourget.—Four, MCZ 19714, SL 24.6–28.5 mm., Brazil, State of Amazonas, Lagôa, Saracá, Silves, near Serpa (Itacutiara), 1865–1866, Thayer Expedition, Stephen Van Renssalaer.—Two, MCZ 19861, SL 21.0–21.5 mm., Brazil, State of Pará, Santarém, 1865–1866, Thayer Expedition, Bourget.—Seven, MCZ, 19646, SL 17.5–27.4 mm., Brazil, State of Pará, Obidos, 1865–1866, Thayer Expedition, Col. Bentos.—One, MCZ 19765, SL 27.4 mm., Brazil, State of Amazonas, Lake Hyanuary, near Manáos, 1865–1866, Thayer Expedition, M. Navez.—Thirteen, MCZ 19965, SL 24.0–27.5 mm., Brazil, State of Amazonas, Codajáz, 1865–1866, Thayer Expedition, Bourget.—Four, MCZ 19978, SL 25.4–30.5 mm., Brazil, Juturana, 1865–1866, Thayer Expedition.—Two, MCZ 19998, SL 25.7–27.0 mm., Brazil, Curupira, 1865 or 1866, Thayer Expedition, Major Coutinho.—One, SU 21964, SL 24.4 mm., and four CAS(IUM) 11688, SL 21.6–25.5 mm., British Guiana, Konawaruk, Essequibo River, 1908, Carl H. Eigenmann.—Three, CAS(IUM) 11690, SL 24.9–27.0 mm., British Guiana, Essequibo River at Rockstone, 1908, C. H. Eigenmann.—Five,

CAS(IUM) 11690, SL 19.5–23.7 mm., British Guiana, Essequibo River at Gluck Island, Sept. 30, 1908, C. H. Eigenmann.—Two, SU 50234, SL 25.0–27.0 mm., British Guiana, no other data.—Four, SU 50225, SL 29.4–35.4 mm., aquarium specimens, no other data.—Three, SU 50224, SL 25.8–32.5 mm., aquarium specimens, alizarin preparations, no other data.

Discussion

In the course of this study three major problems have become apparent. The first of these is that of generic allocation; the second and really inseparable one is the relationships among the species; and the third and largest problem, left largely unworked by this study, is geographical variation and subspeciation. To untangle the nomenclatural mixup and mistaken identifications of past authors has presented some minor difficulties, and the conclusions reached are presented in the synonymies above.

Generic designation has proved difficult; indeed, I have believed at times that perhaps it would be best to place all generic and subgeneric taxa treated here under *Nannostomus*, following Sterba and Tucker (1962). However, it seems that to do this would obscure valid differences and relationships. It appears that the only valid difference between *Nannostomus* and *Poecilobrycon* is the presence or absence of a sensory tube in the second orbital bone. This difference seems small, but it proved to be remarkably constant in all specimens examined. The only other character found to correlate with this was a tendency for a longer snout in *Poecilobrycon* than in *Nannostomus*. However, measurements show an overlap in snout lengths even though individual bones of the snout region always seemed broader and relatively shorter in *Nannostomus* than *Poecilobrycon*. Both *Poecilobrycon eques* and *Poecilobrycon unifasciatus* are obviously closely related because of their caudal fin structure and swimming habits. Their tendency toward long snouts and their possession of tubed second infraorbital bones indicate a relationship with *Poecilobrycon harrisoni*. Indeed, the living color pattern of *unifasciatus* suggests relationships both with *harrisoni* and *eques*. These facts made it seem desirable to place these fishes under the genus *Poecilobrycon* with *Nannobrycon* as a subgenus for *unifsaciatus* and *eques*. The color pattern of *P. harrisoni* suggests relationships with *Nannostomus beckfordi*, and it is possible that they had a common ancestor. It thus seems that *Poecilobrycon* is most closely related to that section of the *Nannostomus* containing *beckfordi*.

A few groupings can be determined in *Nannostomus* itself. *Nannostomus trifasciatus* and *marginatus* are obviously closely related in color pattern and anal fin structure; indeed, a separate subgenus could be erected for their reception but I do not believe it advisable. *Nannostomus espei* appears apart from all other members of this genus in hav-

ing the shape of certain scales and the color pattern similar to those of pyrrhulininans. However, a generic or subgeneric name does not seem advisable for this species. Whether these pyrrhulinian-like characters of *espei* indicate an archaic nature is problematical. I am inclined to believe that they are, especially when one considers that the body shape of this species is more like that of pyrrhulininans than any other nannostominan. On the other hand, it lacks the tube in the second orbital bone that is present in *Poecilobrycon* and the pyrrhulininans. Presumably the presence of this tube is a primitive character for nannostominans. It is possible that the loss of the tube in *espei* was independent of its loss in other species of *Nannostomus* and that my association of *espei* with species of *Nannostomus* rather than with *Poecilobrycon* is artificial. The problem cannot be settled with the morphological data at hand.

Nannostomus digrammus is likewise apart from other species of *Nannostomus* in the highly modified anal fin of the male. It appears, on basis of color pattern and premaxillary teeth, to be more closely related to *beckfordi* and *bifasciatus* than to any other known nannostominan.

Both *N. beckfordi* and *N. bifasciatus* appear related. They lack specialized or distinctive characters that set the other species of *Nannostomus* apart from them. They both lack an adipose fin; apparently both have at least some perforated lateral-line scales and have only moderately modified anal fins in the male. Their color patterns are somewhat different. However, until the color pattern and other characters of the widely distributed *beckfordi* can be studied adequately, it will remain difficult to evaluate its relationship with *bifasciatus*.

Concerning geographical variation within a species, *N. espei*, *N. bifasciatus*, and *P. harrisoni* appear to have restricted ranges, and little or no geographical variation was noted in the specimens utilized in the present study. *Nannostomus beckfordi*, *digrammus*, *trifasciatus*, *marginatus*, *Poecilobrycon unifasciatus*, and *eques* have a wide distribution in South America. Of these, *beckfordi* and *marginatus* were noted to have the greatest geographical variation. Indeed *beckfordi* is so variable that future work based on sufficient collections may show good reasons to recognize many subspecies and perhaps even species of this group of related populations.

Although some morphological, especially live color, variation correlated with geographical distribution was noted in *marginatus*, the close relationship of these population samples seems clearer than those of *beckfordi*. Some degree of difference was found in specimens of *trifasciatus* from Peru and British Guiana and this, it seemed, could be correlated with color differences in aquarium specimens said to have

come from these respective areas. However, the source of the specimens was never reliable enough for serious consideration.

Insufficient specimens of *digrammus* in good condition were at hand to consider geographical variation in color pattern or other characters.

The presence or absence of an ocellus in *unifasciatus* seemed geographically correlated, along with a few other characters. Undoubtedly *ocellatus* and *unifasciatus* will be recognized as subspecies when sufficient study material becomes available.

Poecilobrycon eques seems remarkably constant over its large range from Peru to British Guiana. Both color pattern and morphology of preserved specimens seem quite stable, and I have not noticed any differences in live specimens said to be imported from Peru and British Guiana.

Summary

The characid subtribe Nannostomina (defined by Weitzman, 1964) contains two genera, *Nannostomus* and *Poecilobrycon*. *Poecilobrycon* is divided into two subgenera, *Poecilobrycon* and *Nannobrycon*. *Nannostomus* consists of six known species, *Poecilobrycon* of three, with two of these in the subgenus *Nannobrycon*. The species are as follows:

Nannostomus espei (Meinken)
Paruma River, British Guiana.

Nannostomus beckfordi Günther
British Guiana, south through French Guiana, and Surinam, and in the Amazon Basin as far west as the Rio Negro.

Nannostomus bifasciatus Hoedeman
Surinam River, Surinam.

Nannostomus digrammus Fowler
Rupununi district of British Guiana and west into Brazil as far as the Rio Negro.

Nannostomus trifasciatus Steindachner
British Guiana, westward and south into the Amazon Basin as far as the Pébas district of Peru.

Nannostomus marginatus Eigenmann
British Guiana, southward into the Amazon Basin and as far west as the Caquetá Province of Colombia.

Poecilobrycon harrisoni Eigenmann
Demerara River, British Guiana.

Poecilobrycon unifasciatus (Steindachner)
British Guiana, Rio Negro in Brazil north to Rio Orinoco in Venezuela.

Poecilobrycon eques (Steindachner)
British Guiana south into Amazon Basin and west to Pébas region of Peru, Rio Negro north to Caicara in Venezuela.

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